1996

Genetic Components of (Co)variance for Postweaning Growth, Carcass Composition and Meat Quality Traits Among Brahman-Influenced Beef Steers.

D. H. denny Crews Jr
Louisiana State University and Agricultural & Mechanical College

INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

UMI

A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor MI 48106-1346 USA
313/761-4700 800/521-0600

GENETIC COMPONENTS OF (CO)VARIANCE FOR POSTWEANING GROWTH, CARCASS COMPOSITION AND MEAT QUALITY TRAITS AMONG BRAHMAN-INFLUENCED BEEF STEERS

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy
in
The Interdisciplinary Program in
Animal and Dairy Sciences

by

D.H. "Denny" Crews, Jr.
A.A., South Florida Community College, Avon Park, 1987
B.S., University of Miami, Coral Gables, 1989
M.S. in Animal Science (Breeding and Genetics), University of Florida, 1992
December, 1996

DEDICATION

This manuscript is dedicated to the memory of the late Dr. Don Darryl Hargrove, Professor of Animal Science, University of Florida, who was major professor and friend during my pursuit of the degree of Master of Science. My advanced study of the genetics of beef cattle has often been guided by Dr. Hargrove's example; he was among the few who always provided a source of encouragement, but also reminded me of the value of the things I know. His character as a teacher was not merely to give instruction but to inspire the search for knowledge. To Dr. Hargrove, above all, I credit my true understanding of a passage which has guided me through higher academia:

A wise man will hear, and will increase learning; and a man of understanding shall attain unto wise counsels.

Proverbs 1:5

ACKNOWLEDGEMENTS

The author wishes to express sincere thanks to his degree supervisory committee. Serving as major advisor and chairman, Dr. D.E. Franke, Professor of Animal Science, deserves special note. Without his patience and willingness to allow the author to explore new things, this dissertation would not have been possible in its present scope. Also, the author wishes to thank the remaining members of the degree committee: Dr. P.E. Humes, Professor and Head, Department of Animal Science, and Dr. R.W. Adkinson, Professor of Dairy Science, who were both valuable advisors and friends to the author throughout his degree program, and especially during the preparation of this manuscript. Further, Dr. E. Barry Moser, Associate Professor of Experimental Statistics, served as minor professor and provided crucial insight into the methodological interpretation of these analyses. Dr. Moser is credited for being among the few statistics professors who are always understandable. The author would finally like to thank Dr. David W. Foltz, Associate Professor of Zoology, who participated as professor for the minor program in Interdisciplinary Studies in Genetics, and was also a valued member of the degree supervisory committee. The service of Dr. W.G. Henk, Associate Professor of Veterinary Anatomy, as dean's representative to the committee is also recognized.

Additionally, Dr. L. Dale Van Vleck, Professor of Animal Science, University of Nebraska, Lincoln, deserves special thanks for providing the

author with the opportunity to gain valuable experience as a visiting scientist with the UNL statistical genetics group during crucial stages of data analysis and preparation of the manuscript contained herein.

Without the help, fellowship and friendship of the graduate students of the Departments of Animal Science and Dairy Science, this dissertation would not have been possible; the author will always cherish his friends and colleagues. Of special note among these are Mr. Brian Smith, Mr. Les Walz, Mr. John Cole, Mr. Orlando Habet, Mr. Aaron Higbie, Ms. Lori Smith and Ms. Theresia Knowles. The author also recognizes his friendship with the office staff, student workers and research associates, who, throughout his program, were supportive and helpful. Much credit for the motivation of the author on this particular dissertation topic is due to professionals in academics and the beef industry too numerous to name completely. However, a few of those individuals should be recognized: Mr. Jim Reeves, Executive Director, American Brahman Breeders Association; Dr. Bill Mies, Associate Professor of Beef Cattle Science, Texas A&M University; Dr. Larry V. Cundiff, Breeding and Genetics Research Leader, U.S. Meat Animal Research Center; Mr. Wendell Schronk, Executive Director, Beefmaster Breeders Universal; Dr. John Sullivan, Extension Beef Cattle Specialist, Louisiana Cooperative Extension Service; Dr. Doug Hixon, Extension Beef Cattle Specialist, Department of Animal Science, University of Wyoming; Dr. Jim Sanders, Professor of Animal Science in Beef Cattle Genetics, Texas A&M University; Dr. Keith Gilster,

Professor of Animal Science, University of Nebraska, Lincoln; Mr. Hal Hawkins, Animal Physiologist, King Ranch Cattle Division; Dr. Stanley Kelley, Assistant Professor of Animal Science, Sam Houston State University; Mr. Marcus Shackelford, Rocking S Brahman Ranch, Wauchula, Florida and the American Brahman Breeders Association; and the cattlemen who, through these recent years, have been supportive of my exploration of questions related to the optimal utilization of Brahman genetics in beef cattle production.

For spiritual friendship and guidance, the author extends sincere thanks to Fr. Richard Moore and Fr. Ralph Howe of Trinity Episcopal Church, Baton Rouge, who, throughout his program, provided valuable inspiration and wise counsel, and taught him in all things to seek the comfort and guidance of God: Father, Son and Holy Spirit.

Finally, the author cannot express adequate thanks to his family for their support throughout the long period he spent in graduate school. Without them, he never would have made it.

TABLE OF CONTENTS

LIST OF TABLES

ABSTRACT

A genetic analysis was conducted on preweaning and postweaning growth and carcass composition records from steers produced in two long term crossbreeding studies. In phase I, Angus (A), Brahman (B), Brangus (BR), Charolais (C) and Hereford (H) sires produced straightbred, F_1, back-cross, three-breed cross and 2- and 3-breed rotational crossbred steers (N = 708) from 1960 to 1968. Straightbred, F_1, back-cross, 3-breed cross and 2-, 3- and 4-breed rotational crossbred steers (N = 1530) were produced from 1970 to 1988 by A, B, C and H sires in phase II. Direct and maternal additive and non-additive genetic effect contrasts were obtained. Heritabilities and genetic and phenotypic correlations were estimated for phase I using a multivariate mixed sire model and for phase II using an animal model. Direct additive genetic effects of B were smaller than the other direct additive genetic effects for hot carcass weight, total lean yield, marbling score and tenderness but not different than the average non-Brahman additive genetic effect for carcass weight adjusted ribeye area. Maternal additive genetic effects were smaller than direct additive genetic effects for carcass traits. Direct heterosis effects involving B were positive and larger than heterosis effects not involving B. Maternal heterosis effects were near zero for carcass traits. The ranking of genetic effects in phases I and II were similar. Heritability estimates for postweaning growth and carcass traits were moderate to large, except in the case of daily gain on ryegrass, which had a low heritability. Genetic

correlations indicated a high association among weights, rates of gain and total lean yield. Increased growth and carcass weight had negative phenotypic and genetic correlations with carcass weight adjusted ribeye area. Genetic correlations among fat and meat quality traits were small, although the association between marbling score and Warner-Bratzler shear force tended to be favorable. Preweaning growth traits had positive correlations with carcass traits related to weight and total lean yield. Increasing percentage B was a significant source of heterogeneity among estimates of genetic and phenotypic (co)variances for ribeye area and Warner-Bratzler shear force.

CHAPTER 1

INTRODUCTION

Crossbreeding has become the predominant system of mating in the United States beef industry. By providing for the use of additive and non-additive variation among breeds, crossbreeding, along with accurate selection practices, can significantly improve the efficiency of the beef production enterprise.

The beef industry in the United States is extensive and segmented. The beef industry consists of the preweaning phase, backgrounding phase, finishing phase and the packing phase. Often, the traits associated with profitability in each of these phases are different. That is, cattle which are optimal or desirable in one phase may be extreme or undesirable in the other phases.

In the Gulf Coast Region of the United States, the cow-calf (preweaning) production system is the most common segment of the beef cycle. The environmental conditions of this region have been characterized as sub-tropical. A major proportion of the cow-calf segment of the U.S. beef industry is located in this region, where mild winter and longer, humid summer seasons mandate the use of germ plasm resources that are readily adaptable to extensive, forage-based management programs. The need for cattle adapted to the sub-tropical environment of the Gulf Coast Region of the United States has resulted in the extensive use of crossbreeding with zebu type

cattle, especially Brahman. Cow-calf producers must optimize productivity of weaned calves but maintain marketability; therefore, a large percentage of cows produced in this region have some Brahman breeding. Crossbreeding systems which utilize a high percentage of Brahman or *Bos indicus* influence produce calves that have distinct zebu characteristics. These characteristics include longer ears, loose skin, especially about the head and neck, and evidence of cervico-thoracic hump. Additionally, certain hair coat colorations, such as gray and brindling, are associated with *Bos indicus* breed composition. These calves are often discriminated against by the feeder and packer segments of the beef industry. The price discrimination can be attributed to less desirable USDA yield and quality grades and measures of tenderness often perceived to be associated with cattle containing Brahman influence. The reduced price received for high-percentage Brahman calves has prompted investigation of alternative crossbreeding systems which moderate the level of Brahman influence, but maintain the adaptability of the cow herd to sub-tropical environments. These systems include the use of Brahman-derivative sire breeds in crossbreeding, the use of composite mating systems, and the use of tropically adaptable *Bos taurus* breeds.

Crossbreeding systems utilizing the Brahman breed and its derivatives provide for beneficial heterosis levels in traits associated with reproduction and growth, improved resistance to parasites, and increased longevity in the cow herd. The preweaning segment of the beef cycle can be significantly improved

with the use of Brahman influenced cattle. However, traits associated with postweaning growth, carcass composition and meat quality have been shown in most cases to be negatively impacted by high levels of Brahman influence. The present challenge to the beef industry in the Gulf Coast Region is to optimize the use of Brahman genetics.

Beef cattle improvement programs have traditionally focused on live animal growth traits. However, as value-based marketing systems continue to develop, and as consumers become more concerned with diet-health issues, the relative importance of body composition traits will increase. Traits associated with carcass composition and meat quality currently have more impact on profitability of production than ever before. Consumers continue to express their desire to purchase leaner beef, but also beef that is consistent and acceptable in palatability. These trends have resulted in an increased need for research on how management and genetics impact carcass composition and meat quality.

Of particular interest are genetic (co)variances among traits of economic importance to the total production cycle. It has been shown (Marshall, 1994; MacNeil et al., 1984) that genetic antagonisms exist between traits associated with preweaning performance and those associated with postweaning performance and carcass merit. The diverse and extensive environments under which calves are produced, in contrast to the relatively uniform and intensive environments characteristic of the finishing phase of the beef cycle makes the

estimation of these genetic relationships important. However, as cattle types and production alternatives change, the relationships among traits of economic importance to the beef industry must be periodically reevaluated.

Estimates of genetic parameters are essential to the evaluation of potential mating and selection strategies. There is a current lack of carcass information in the beef industry that can be traced to genetic origin (NCA, 1992).

Heritability, or the proportion of phenotypic variability due to variance in additive genetic effects, indicates the response potential of a particular trait to selection. Further, the genetic correlations among traits of interest must be considered so that antagonisms among traits of economic interest may be minimized under selection.

Until recently, the estimation of additive genetic merit, or breeding value, has been limited to data from purebred lines. Advances in estimation methodology and computing power have extended the ability of researchers to obtain estimates of additive genetic value and genetic covariances from crossbred data. The application of mixed-model methods to crossbred data has become the standard procedure for genetic parameter and breeding value estimation in both field data and research data. Most commercially important beef cattle breeds currently publish summaries of breeding values for active sires within that breed. However, across-breed evaluations are not currently available, or are available only in specific cases. Also, few breeds have

included evaluation of carcass traits. Further research is therefore needed in the area of genetic parameter estimation for carcass traits and genetic analysis of crossbred beef cattle data.

Heritability estimates from the recent literature are generally moderate to large for carcass traits, indicating that these traits would respond to selection. Currently, no studies have reported data from experiments where cattle were selected on the basis of carcass composition. Reports of the genetic covariance among carcass traits, or between carcass traits and pre- or post-weaning traits, are needed for cattle with Brahman influence.

The objectives of the present studies were to estimate genetic parameters associated with traits from each segment of the beef production cycle, and to estimate the genetic and phenotypic (co)variances and correlations among those traits; to evaluate the influence of fixed effects on the estimation of these parameters; and to explore new procedures for the estimation of the effects of Brahman influence on genetic variability.

CHAPTER 2

REVIEW OF LITERATURE

Carcass traits including yield, composition, palatability and quality are important in the evaluation of breeds and breed combinations for beef production. Crossbreeding is widely used in the U.S. beef industry to increase production. Reviews by Cundiff (1970), Franke (1980), Gregory and Cundiff (1980), Long (1980) and Turner (1980) have indicated that crossbreeding is an effective tool to make use of additive genetic variation among breeds and to generate heterosis. To determine which breeds and breed combinations should be involved in crossbreeding systems, it is necessary to have estimates of transmitted or additive effects of breeds and of expected heterosis levels in breed combinations. The influences of breed direct additive and heterosis effects as well as maternal additive and non-additive effects on postweaning growth, carcass composition and meat quality traits are important considerations in designing effective crossbreeding systems for beef cattle.

In the Gulf Coast Region of the United States, the Brahman breed has been used extensively in crossbreeding programs designed to increase adaptability to the subtropical climate and to increase preweaning performance of calves that are marketed at weaning. Several studies have shown that carcasses from cattle with heavy Brahman influence grade lower in regard to both yield and quality than those from cattle with predominantly *Bos taurus* breeding.

Thermal stress limits the efficiency of the feedlot operation in the Gulf Coast Region of the United States. Under thermal stress, the efficiency of uptake of potentially absorbable nutrients is greatly decreased by a reduction in dry matter intake, slightly increased due to greater ruminal retention time, and decreased by reduced blood flow to the digestive tract (Beede and Collier, 1986). The use of Brahman and Brahman crossbreds for beef production has been one method of maintaining performance under thermal stress. Finch (1986) stated that cattle with *Bos indicus* breeding have a greater ability to lower internal resistance to heat transfer during times of thermal stress. Also, the resistance of sleek, dense hair coats, common among the Brahman and its crosses, to inward heat flow is a factor in maintaining thermal equilibrium. The efficiency with which cattle regulate internal temperature is dependent on breed or biological type, among other factors (McDowell, 1958). Warwick (1958) suggested that zebu cattle perform without thermal stress in a temperature range from 10 to 27°C, and failure of their heat regulation mechanism does not occur until 35°C. Brody (1956) indicated that European breeds performed best at lower temperature ranges than zebu breeds (-1 to 15°C) and thermal stress also occurred at lower temperatures (27 C). Crockett et al. (1979) stated that tolerance to higher temperatures among Brahman and Brahman crossbred cattle has been well established.

Many researchers have reported that Brahman crossbred feeder calves are often heavier at weaning than their *Bos taurus* contemporaries. Initial feedlot weight of Brahman-sired steers was shown by Crockett et al. (1979) to be heavier than that of Beefmaster-, Brangus-, Limousin-, Simmental- and Maine-Anjou-sired steers. Crockett and coworkers further showed that steers produced by Brangus dams were heavier at weaning and at the beginning of the postweaning feeding period than steers produced by Hereford and Angus dams. Young et al. (1978) reported that Brahman-sired steers were 17 to 26 kg heavier at 200 d of age than steers sired by Hereford, Angus, Devon and Holstein bulls. Also, Cundiff et al. (1984) reported heavier initial feedlot weights for Brahman-sired steers than for Tarentaise-, Pinzgauer-, Hereford-, Sahiwal- and Angus-sired steers.

Huffman et al. (1990) compared steers of known percentages of Angus and Brahman breeding and showed that increased Brahman breeding was associated with heavier initial feedlot weights. The 1/2- and 3/4-Brahman steers were approximately 40 kg heavier at the beginning of the feedlot period than 1/4-Brahman and straightbred Angus steers. Lopes (1986) however, reported no difference in the initial feedlot weights of F1 Brahman-Hereford steers and straightbred Hereford steers.

Rate of gain during the feedlot period is a postweaning growth trait of economic importance. Research has shown that cattle of differing biological type (breeds) and physiological maturities vary in their ability to grow and

utilize feed. Comerford et al. (1988) reported significant levels of heterosis (5.6 to 8.1 %) for feedlot gain in crosses of the Brahman with the Simmental, Limousin and Polled Hereford breeds. These findings were in agreement with those of Peacock et al. (1982) who showed an overall heterosis level of 9.3% for feedlot gain in Brahman x Angus and Brahman x Charolais crossbred steers. Crockett et al. (1979) reported higher rates of gain in Brahman-sired crossbred steers than in steers sired by Limousin, Simmental, Beefmaster and Brangus bulls. In a diallel mating among Angus, Brahman and Charolais, Peacock et al. (1982) reported that straightbred Brahman steers gained slower in the feedlot than other breed types, but Brahman crossbred steers gained faster than Angus and Charolais crossbreds. These studies compared steers fed for a constant number of days. On the other hand, Carpenter et al. (1961) compared the feedlot performance of steers of known percentages of Brahman and Shorthorn breeding that were fed for 140 d. They reported that average daily gains on feed were not different among steers of 25, 50, 75 and 100 % Brahman breeding. Carpenter and coworkers also noted that there was a need for comparison of Brahman and Brahman crossbreds, and for data evaluating the effects of increasing percentages of Brahman breeding on slaughter and carcass characteristics.

Sanders and Paschal (1987) compared steers from Senepol, Angus and zebu sires that were fed for 135 d. The steers sired by Angus and Senepol bulls gained at a similar rate, but both groups gained faster than the zebu

crosses. Zebu-sired steers were the heaviest at the end of the feeding period. Angus-sired steers were fatter than the zebu sired steers.

Cundiff et al. (1984) compared the feedlot performance of steers produced from the mating of Angus and Hereford cows to Angus, Hereford, Tarentaise, Pinzgauer, Brahman and Sahiwal bulls. Steers were serially slaughtered following constant numbers of days on feed. They reported that the average daily gains in the feedlot were similar among Tarentaise-, Pinzgauer-, Hereford- and Angus-sired steers, however, the Brahman- and Sahiwal-sired steers gained at a faster rate than the *Bos taurus* steers. In a similar study, Koch et al. (1982) compared steers at constant age, weight, fat thickness, fat trim and marbling end points. At a constant age end point of 445 d, Brahman crossbred steers had heavier final live weights than other breed types. At a 1.25 cm fatness end point, Brahman crossbred steers were intermediate in final live weight to the heavier Tarentaise and Pinzgauer crosses and the lighter Angus-Hereford reciprocal crosses.

Huffman et al. (1990) compared feedlot performance of steers of known percentages of Brahman and Angus breeding and fed to four outside fat end points. The ½- and 3/4-Brahman steers gained faster on feed and had heavier final feedlot (slaughter) weights than the 1/4-Brahman and Angus steers. Lopes (1986) showed that F_1 Brahman-Hereford steers gained faster than straightbred Hereford steers when both were fed to an outside fatness of 1.0 cm. However, the work of Cesar (1984) showed that the final weights among

among steers visually classified as Brahman x European or European x European crosses were not different.

Efficiency of cattle on feed can be expressed as the ratio of feed intake to weight gain. Cundiff et al. (1984) reported no significant differences in Mcal ME/kg gain among steers sired by Tarentaise, Pinzgauer, Sahiwal, Angus, Hereford and Brahman bulls when adjusted to a constant time on feed. Other researchers have shown that cattle with Brahman breeding did not differ in their ability to convert dry matter to gain from cattle possessing only *Bos taurus* breeding (Cesar, 1984; Huffman et al., 1990). Cundiff and Gregory (1968) stated that more than half of the variation in weight gain on feed was due to non-genetic factors.

Many researchers have compared Brahman and Brahman crossbred cattle with *Bos taurus* contemporaries when slaughtered at various feeding end points. The need for studies comparing cattle at similar physiological and compositional end points has been noted (Johnson et al., 1990); however, genetics studies often compare carcass characteristics after cattle have been slaughtered at constant age or time on feed end points. The National Beef Quality Audit (NCA, 1992) indicated that from 1972 to 1991, outside fatness had changed very little in the beef industry. Zinn et al. (1970) showed that length of feeding period was positively correlated with dressing percentage and

the deposition of external fat, regardless of genotype. Comparing cattle at a variety of slaughter end points enables researchers to evaluate carcass characteristics equitably.

Heterosis estimates for hot carcass weights were reported by Comerford et al. (1988) to be approximately 10 %, and by Peacock et al. (1979) to be near 20 %. Comerford and coworkers were working with crosses from a diallel among the Polled Hereford, Limousin, Simmental and Brahman breeds, while Peacock and coworkers were evaluating F_1 Brahman-Angus steers. Peacock et al. (1979) concluded that the direct effect of Brahman breeding added 2.3 kg to hot carcass weight. Other researchers have also found that Brahman crossbred steers had heavier hot carcass weights than their *Bos taurus* contemporaries when compared after constant feeding periods (Koch et al., 1982; Young et al., 1978). Huffman et al. (1990) reported that among steers with 0, 25, 50 and 75 % Brahman breeding, the 1/2- and 3/4-Brahman steers had heavier hot carcass weights than the Angus and 1/4-Brahman steers when compared at four outside fat endpoints. Peacock et al. (1979) reported that chilled carcass weights of Brahman, Charolais and Angus steers were 207, 258 and 196 kg, respectively. Brahman x Charolais steers had the heaviest carcasses (258 kg) among six reciprocal breed crosses, followed by Charolais x Brahman (253 kg), Brahman x Angus (246 kg), Angus x Charolais (246 kg), Angus x Brahman (235 kg) and Charolais x Angus (233 kg). Koch et al. (1982) reported that Brahman-sired crossbred steers ranked highest for

carcass weight (age-constant basis) at 306 kg followed by Tarentaise-, Angus-, Hereford-, Pinzgauer- and Sahiwal-sired steers. Lopes (1986), however, found no difference in the hot carcass weights of F_1 Brahman-Hereford and Hereford steers fed to 1.0 cm outside fat. His findings were in agreement with those of Cesar (1984) who also reported similar hot carcass weights among Brahman-European and European crossbreds fed to 1.0 cm outside fat. Sanders and Paschal (1987) reported that carcass weights of Angus-sired steers were approximately 15 kg lighter than those of zebu-sired steers after 135 d on feed.

Studies have shown that cattle with Brahman influence have smaller gastrointestinal tracts relative to body weight than cattle with only *Bos taurus* breeding (Huffman et al., 1990; Lopes, 1986; Carpenter et al., 1961). Often researchers reported similar slaughter weights for cattle and subsequently different hot carcass weight rankings among breeds, or differences in dressing percentage, indicating differences in gastrointestinal fill. Sanders and Paschal (1987) stated that zebu-sired steers had heavier hot carcass weights, and therefore higher dressing percentages than Angus- and Senepol-sired steers. Huffman et al. (1990) reported that their 3/4-Brahman steers had less rumen fill than their 1/4-Brahman steers. Carpenter et al. (1961) found progressively lower rumen fill with increases in percentage Brahman breeding from 25 to 100%, however, there were no significant differences in dressing percentage among the breed groups.

Comerford et al. (1988) compared steers from a diallel among the Brahman, Polled Hereford, Limousin and Simmental breeds and reported that at an average slaughter age of 445 d, the Brahman cross steers were fatter (1.03 cm) than Limousin (0.88 cm) and Simmental (0.82 cm) but not as fat as Polled Hereford (1.23 cm) cross steers. Crockett et al. (1979) found, following constant feeding periods, that Brahman, Beefmaster and Brangus cross steers were fatter than Limousin, Maine Anjou and Simmental crosses. Peacock et al. (1979) likewise reported that Brahman-Angus carcasses were fatter than those from Angus, Brahman and Charolais crossbred steers. Further, Peacock et al. (1982) reported a direct effect of Brahman breeding of +0.18 cm for subcutaneous fat thickness.

The area of the longissimus (ribeye) muscle at the 12-13th rib interface is the most common measure of muscling in beef cattle, and is the only measure of muscularity used to calculate USDA yield grade (USDA, 1989). Comerford et al. (1988) reported heterosis estimates from 6.2 to 10.3 % for ribeye area. Further, Comerford and coworkers found that at a constant slaughter age, Brahman cross steers had ribeye areas which were 10 cm^2 smaller than those of Limousin and Simmental cross steers, but that the Brahman cross steers also had smaller carcasses. These results were in agreement with the work of Crockett et al. (1979) who reported that Brahman and Brahman-derivative sires produced steers with ribeye areas that were smaller than steers produced by Maine-Anjou, Limousin and Simmental sires.

Sanders and Paschal (1987) and Olson (1987) reported that *Bos indicus* cross steers had larger ribeye areas than steers sired by Senepol bulls. Cesar (1984) found no difference in ribeye area among Brahman-European and European crossbred steers, Lopes (1986) also showed that Hereford and F_1 Brahman-Hereford steers had similar ribeye areas. Huffman et al. (1990) found that ribeye area did not differ among steers of known percentages of Angus and Brahman breeding; however, 1/4-Brahman and straightbred Angus steers had larger carcass-weight adjusted ribeye areas than did ½- and 3/4-Brahman steers. Similarly, Peacock et al. (1979) showed that Angus steers had larger carcass-weight adjusted ribeye area than steers of other breed types involving Brahman in a study of the Brahman, Angus and Charolais breeds. Lopes (1986) found that ribeye area per 100 kg hot carcass was larger among Hereford than among F_1 Brahman-Hereford steers. Sanders and Paschal (1987) reported that ribeye area per kg hot carcass was equal (0.256 cm^2) among Senepol- and zebu-sired steers, but Angus-sired steers had larger carcass-weight adjusted ribeye area (0.266 cm^2). Crews (1992) reported that Simmental-sired steers had larger ribeye area than F_1 Brahman-Angus, Braford- and Simbrah-sired steers, but, at 1.0 cm outside fat, carcass weight adjusted ribeye area was similar among the breed types. Similarly (Crews, unpublished data, 1995) found that total carcass yield was more closely related to carcass-weight adjusted ribeye area than actual ribeye area, and may therefore be a better indicator of total carcass muscling.

Fat deposited in the kidney, pelvic and heart regions of the carcass (KPH) is commonly measured as a percentage of carcass weight, and is included in the USDA yield grade equation as an estimate of internal or visceral fat (USDA, 1989). Breed differences in KPH have been shown to exist, but results are conflicting. Following a constant feeding period, Comerford et al. (1988) reported that Polled Hereford steers tended to have more internal fat than Brahman, Limousin and Simmental steers, although the differences were small. Cesar (1984) also reported that European crossbred steers tended to have more KPH than Brahman-European crossbred steers. Huffman et al. (1990) found no significant difference in KPH fat among steers of 0, 25, 50 and 75 % Brahman breeding.

The USDA yield grade equation is used to estimate the percentage of carcass weight that can be expected to be derived in the form of boneless, closely trimmed retail cuts from the primal loin, round, rib and chuck regions of the carcass (USDA, 1989). Yield grade is readily controlled by management system, due to a high impact of fatness on final yield grade. Fatter, heavier and less muscular carcasses receive higher (less desirable) yield grades, while lower yield grades indicate carcasses that are leaner, weigh less and are more muscular. Comerford et al. (1988) and Crockett et al. (1979) reported that the yield grades of Brahman crossbreds were higher than those of continental breed-sired steers and more desirable than those of British-type steers. Huffman et al. (1990) showed that the yield grades of 3/4-Brahman steers

were less desirable than those of Angus, 1/4- and 1/2-Brahman steers. Crews (1992) found no differences in USDA yield grade among steers sired by Angus, Brahman, Simbrah, Senepol and Simmental bulls when compared at a constant outside fat end point of 1.0 cm.

Morgan et al. (1991) stated that the single most important consumer component of beef palatability or eating quality was tenderness. Tenderness is typically measured objectively by the force required to shear a core from cooked muscle using a Warner-Bratzler shear device. Also, trained sensory panels have been employed to evaluate tenderness, in addition to other sensory attributes of meat. Many researchers have found that cattle with Brahman or *Bos indicus* breeding produced meat that was less tender than did cattle with only *Bos taurus* breeding. Lopes (1986) reported that the Warner-Bratzler shear (WBS) values among F1 Brahman-Hereford steers were 1.5 kg higher than those among straightbred Hereford steers fed to 1.0 cm outside fat. This was in agreement with the work of Cesar (1984), who reported that Brahman-European crossbreds had less tender loin steaks than European-European crossbreds. Several researchers have shown that an increase in percentage Brahman or *Bos indicus* influence was associated with increased WBS values and decreased sensory panel tenderness ratings (Pringle et al. 1995; Shackelford et al., 1991; Huffman et al., 1990; Crouse et al., 1989; Carpenter et al., 1961). Koch et al. (1982) found that 14 % of Brahman and 20 % of Sahiwal crossbreds fell below desirable tenderness levels, and that

Bos indicus cattle were more variable in tenderness than *Bos taurus* cattle. Higher activity of calcium dependent protease inhibitor (calpastatin) has been implicated in contributing to the lack of postmortem tenderization associated with cattle of heavy *Bos indicus* influence (Shackelford et al., 1994; Wheeler et al., 1990; Whipple et al., 1990). A review of Brahman influence on tenderness and meat quality is given by Crews (1995).

USDA quality grades contribute significantly to the determination of carcass value. Young beef carcasses (less than 24-30 mo of age) which typically receive the USDA "A" maturity score vary in quality grade primarily due to marbling score. Brahman breeding has been associated with lower marbling scores. After constant feeding periods, several researchers have reported that cattle with Brahman breeding produce carcasses with less intramuscular fat, or marbling, than cattle without Brahman influence (Comerford et al., 1988; Koch et al., 1982; Peacock et al., 1982). Crouse et al. (1989) showed that increased percentages of Brahman and Sahiwal breeding were associated with lower marbling scores. This was supported by the work of Huffman et al. (1990) who reported lower marbling scores for cattle with increased percentages of Brahman influence. In a study where steers were fed to a subcutaneous fat end point of 1.0 cm, Lopes (1986) reported no difference in marbling score among Hereford and F1 Brahman-Hereford steers. Likewise, Crews (1992) found no differences in marbling scores among composite steers sired by Brahman, Braford, Simbrah, Senepol

and Simmental steers fed to 1.0 cm outside fat. These researchers implied that constant fat end points tended to reduce among-breed variation in marbling score. Cesar (1984) also found marbling scores and quality grades among Brahman-European and European-European crossbred steers to be similar.

Heterosis is defined as the difference in phenotypic performance between crossbred progeny and their purebred parents due to non-additive genetic effects based on expected breed heterozygosity. Urick et al. (1974) found no difference for carcass weight per d of age between Angus and Hereford steers (0.56 vs 0.562 kg), however, percent heterosis was important ($P < .05$) for carcass weight per d of age (5.6%) for the reciprocal crosses of these two breeds. Heterosis was also significant for carcass weight among reciprocal crosses of Hereford and Angus in the study of Long and Gregory (1975). Bertrand et al. (1983) and Baker et al. (1984) reported similar carcass weights for Angus and Hereford steers and bulls, while Angus x Hereford reciprocal crosses had heavier hot carcasses than the straightbred average. Marshall (1994) summarized research conducted to evaluate direct and maternal heterosis effects on carcass traits. Based on twelve studies, he reported that direct heterosis was positive and generally significant for carcass traits. Heterosis increased hot carcass weight, fat thickness and total lean yield an average of 10.1, 6.5 and 6.6 %, respectively. Heterosis increased ribeye area 4.1 % and marbling score 3.8 % in the summary of Marshall

(1994). He likewise found that direct heterosis decreased yield grade (increased yield) and Warner-Bratzler shear force (increased tenderness) by 0.6 and 6.7 percent, respectively. Marshall (1994) also reported that the effects of maternal heterosis on carcass traits were generally small and near zero in most cases with the exception of fat thickness, which was increased 8.9 percent by maternal heterosis.

Genetic parameters for postweaning growth and feedlot performance have not been extensively reported in the literature. Average daily gain was reported by MacNeil et al. (1991) to have a heritability of 0.38 among crossbred bulls and steers. They also reported a heritability estimate of 0.25 for slaughter weight. Average daily gain on feed had positive phenotypic correlations with feed intake, slaughter weight, and fat thickness. The phenotypic correlation between average daily gain and feed conversion efficiency (metabolizable energy intake per kg gain) was -0.48. Further, MacNeil and coworkers reported that the genetic correlations of average daily gain with feed intake and slaughter weight were positive (Rg = 0.73 and 0.94, respectively).

Genetic parameters for carcass traits have been estimated in a wide variety of cattle types and breeds in the literature. Marshall (1994) stated that the importance of carcass and body composition traits will increase as consumers become more diet conscious and as the beef industry moves toward a value based marketing system. Most researchers have reported

moderate to high heritabilities for carcass traits associated with weight and yield. Other researchers have reported that the heritabilities of meat quality traits were lower than for yield and weight, but these estimates tend to be variable.

The heritability of hot carcass weight was reported by Gregory et al. (1995) to be 0.23 among purebred and composite cattle evaluated at the Meat Animal Research Center in Nebraska. Similar heritability estimates for hot carcass weight were reported by Lamb et al. (1990), Reynolds et al. (1991), Veseth et al. (1993), and Wilson et al. (1993). These researchers all reported the heritability of hot carcass weight to be between 0.31 and 0.38 based on genetic analyses of cattle involving straightbreds, crossbreds and composites. Koch (1978) reported that the heritability of hot carcass weight in 377 Hereford steers from 64 sires was 0.68. Koch et al. (1982) reported a heritability estimate of 0.43 for 2453 Hereford steers sired by 370 bulls. This was similar to the heritability estimate of 0.44 reported by MacNeil et al. (1984). Benyshek et al. (1981) estimated the heritability of hot carcass weight among 8474 Hereford steers to be 0.48. Marshall (1994) reported that the average heritability of hot carcass weight among twelve studies was 0.41.

Fat thickness is a trait that is closely associated with yield grade. Arnold et al. (1991) reported that fat thickness had a heritability of 0.49 in a study of 2411 Hereford steers which were slaughtered at a weight constant

end point. Gregory et al. (1995), reporting genetic parameters for purebred and composite steers, found that the heritability of fat thickness was 0.25 when steers were slaughtered at age constant end points. Similar estimates were reported by Lamb et al. (1990) and Wilson et al. (1993). Koch et al. (1982) reported a moderate to high heritability for fat thickness of 0.41. Heritability estimates for fat thickness of 0.52 were reported by Benyshek (1981) and MacNeil et al. (1991). A high heritability of 0.68 for fat thickness was reported by Koch (1978). Marshall (1994) found that the average heritability estimate for fat thickness among eight studies was 0.44. He stated that heritability estimates for fat thickness tended to be variable, and was related to the variation in slaughter end point.

The only predictor of muscling used in the USDA (1989) yield grade equation is ribeye area, evaluated as the area of the exposed face of the longissimus muscle at the 12th rib region of the carcass. Most researchers reported moderate to high heritabilities for ribeye area. These estimates, reported by Koch et al. (1982), Benyshek (1981), Arnold et al. (1991), Veseth (1993) and Van Vleck et al. (1992), ranged in magnitude from 0.40 to 0.60. Lower heritability estimates for ribeye area were reported by Koch (1978), Lamb et al. (1990), Wilson et al. (1993) and Gregory et al. (1995). These researchers found that the heritability of ribeye area was from 0.22 to 0.32. Few researchers have reported heritabilities for weight-adjusted ribeye area. Heavier carcasses are expected to have larger ribeyes, however, muscling may

differ among carcasses of similar weight. Crews (1995) suggested that carcass weight adjusted ribeye area may be a better indicator of carcass muscling than ribeye area alone since it accounts for differences in hot carcass weight. Huffman (1992) found that ribeye area alone was only a moderately powerful predictor of carcass lean yield.

Reports of genetic parameters for USDA yield grade and estimated percent lean yield in the carcass are variable. Using measures of carcass weight, fatness and muscle size, USDA yield grade estimates the percent of carcass weight expected to be derived as boneless, closely trimmed retail cuts from the four primal regions of the beef carcass. Since yield grade is a "composite" trait, heritability estimates are expected to be variable. Yield grade is most dependent on fat thickness and hot carcass weight. Estimates of muscling and internal fat in the kidney pelvic and heart regions of the carcass account for less than 25 % of the variation in final yield grade (Crews, 1995). Koch et al. (1982) reported the heritability of percent yield to be 0.63. Using Simmental field records, Woodward et al. (1992) reported that yield grade had a heritability of 0.18. Lamb et al. (1990) reported a heritability estimate of 0.23 for yield grade. The estimate of Benyshek (1981) for yield grade (h^2 = 0.49) came from a large study involving the Hereford breed. Marshall (1994), in his review, reported an average heritability for yield grade of 0.36.

Several researchers have reported genetic parameters for total carcass yield. Total lean yield is calculated as estimated percent lean yield multiplied by carcass weight. Similar to yield grade, total lean yield is highly dependent on fat thickness. Therefore, estimates of heritability for this trait in the literature depend on slaughter end point. When steer records were adjusted to 0 mm fat trim, Gregory et al. (1995) reported that total lean yield had a heritability of 0.28. Using carcass data from composite steers produced at the Meat Animal Research Center, Shackelford et al. (1994) reported that retail product yield had a heritability of 0.45. Weight of retail cuts per day of age was reported by Woodward et al. (1992) to have a heritability of 0.30 among Simmental sired steers in a study of Simmental field data. Heritability estimates for total lean yield were reported by Koch (1978), Koch et al. (1982) and MacNeil et al. (1984) to be 0.38, 0.58 and 0.45, respectively. Marshall (1994), summarizing several reports, found that retail product weight had a heritability of 0.47.

Carcass quality depends primarily on USDA marbling score, a visual estimate of intramuscular fat in the longissimus muscle. Cattle slaughtered at an average age of 14 to 24 mo of age, which typically receive the young (A) physiological maturity score are placed into quality grade groups solely on the basis of marbling score. Reports of heritability of marbling score in the literature are numerous. Marshall (1994) summarized thirteen estimates of heritability for marbling score and reported an average of 0.35. His average

was higher than the estimates of Veseth et al. (1993), Wilson et al. (1993), Lamb et al. (1990) and Woodward et al. (1992) who reported the heritability of marbling score to be in the range of 0.23 to 0.33. Heritability estimates from 0.40 to 0.48 were reported for marbling score by Koch et al. (1982), Benyshek (1981), Van Vleck et al. (1992) and Gregory et al. (1995). Koch (1981) reported a heritability of 0.34 for marbling score. Shackelford et al. (1994) measured actual longissimus intramuscular fat content and reported a heritability of 0.93.

Tenderness is measured objectively as the force required to shear a 1.25 or 2.54 cm core from cooked muscle using a Warner-Bratzler shear device. Tenderness has also been measured using trained sensory panels. Van Vleck et al. (1992) reported a heritability of 0.09 for tenderness. Similarly, Gregory et al. (1995) measured tenderness among composite steers and reported a heritability of 0.12. Higher heritability estimates for tenderness were reported by Shackelford et al. (1994) and Koch et al. (1982). Marshall (1994) found that estimates of heritability for tenderness were highly variable in the literature. Summarizing several studies, he found an average heritability of 0.37 for tenderness.

Marshall (1994) found that literature estimates of phenotypic and genetic correlations between preweaning and postweaning growth rate and carcass weight, ribeye area and retail product yield were positive. Correlations of pre- and post-weaning gain with fat thickness and marbling score were also

positive, but generally less strong. Phenotypic and genetic correlations between pre- and post-weaning growth rate and estimated product percent were negative. Growth rate was found to be positively correlated with retail product weight and weight of carcass fat trim. Marshall (1994) further summarized that the phenotypic and genetic correlations of growth rate and tenderness were positive or near zero, as evidenced by negative to near zero phenotypic and genetic correlations between growth rate and Warner-Bratzler shear force. In a single study, Shackelford et al. (1994) found that the calpain proteolytic inhibitor, calpastatin, had negative and favorable genetic correlations with preweaning and postweaning growth rate. This led Shackelford and coworkers to conclude that selection for growth rate would be expected to have a favorable effect on tenderness. Calpastatin inhibition of post mortem proteolysis has been implicated by several researchers as contributing to within and among breed variation in tenderness.

Hot carcass weight was reported by several researchers to have moderate to high and positive phenotypic correlations with longissimus muscle area (Koch, 1978; Koch et al. 1982; Lamb et al. 1990; Veseth et al. 1993; Wilson et al. 1993). Moderately positive phenotypic correlations were also found between hot carcass weight and fat thickness, marbling score, fat trim weight and fat trim percentage by these researchers. Phenotypic correlations between hot carcass weight and retail product weight were high (Rp = 0.84) in the research of Koch (1978) and Koch et al. (1982). As is expected by

inspection of the USDA yield grade equation, phenotypic correlations between hot carcass weight and yield grade, or estimated percent retail yield, were negative (Koch et al. 1982). Strongly positive genetic correlations between hot carcass weight and longissimus muscle area were reported by several researchers (Koch et al. 1982; Lamb et al. 1990; Veseth et al. 1993; Woodward et al. 1993). This correlation was estimated by Koch (1978) to be positive, but near zero (Rg = 0.02). Genetic correlations of hot carcass weight with fat thickness were also reported to be positive by these researchers, with genetic correlation estimates ranging from 0.08 to 0.95. The genetic correlations reported in the literature between hot carcass weight and marbling score were highly variable, ranging from -0.33 (Koch, 1978) to 0.64 (Lamb et al. 1990). Hot carcass weight was reported to have positive genetic correlations with retail product weight, fat trim weight and fat trim percentage (Koch, 1978; Koch et al. 1982), but a negative genetic correlation with estimated cutability percentage (Koch et al. 1982).

Age-constant genetic correlations among carcass traits summarized by Marshall (1994) indicated that selection for reduced carcass fat thickness would be compatible with selection for larger longissimus muscle area and increased cutability. Phenotypic correlations of ribeye area with fat thickness were generally found to be negative and small. Ribeye area was positively correlated with retail product weight, estimated cutability percent and favorably correlated with tenderness (Koch, 1978; Koch et al. 1982; Lamb et

al. 1990; Van Vleck et al. 1992). Phenotypic correlations of longissimus muscle area with marbling score tended to be small (Koch, 1978; Koch et al. 1982; Lamb et al. 1990; Van Vleck et al. 1992; Wilson et al. 1993).

Genetic correlations of ribeye area and fat thickness were negative and small in the reports of Lamb et al. (1990) and Wilson et al. (1993) with values of -0.04 and -0.06, respectively. However, Koch et al. (1982) reported a genetic correlation of -0.44 between ribeye area and fat thickness. Genetic correlations of longissimus muscle area and marbling score were negative, ranging from -0.04 to -0.40 in the studies of Koch et al. (1982), Wilson et al. (1993) and Van Vleck et al. (1992). However, this correlation was estimated to be strongly positive by Lamb et al. (1990) and Veseth et al. (1993) with values of 0.51 and 0.57, respectively. Koch et al. (1982) also reported a positive genetic correlation between ribeye area and estimated cutability.

Koch et al. (1982) and Van Vleck et al. (1992) reported moderately negative genetic correlations between longissimus muscle area and Warner-Bratzler shear force, indicating a favorable relationship between ribeye area and tenderness. Van Vleck et al. (1992) also reported that longissimus muscle area had a negative although weak genetic correlation with tenderness measured by sensory panel evaluation.

Genetic and phenotypic correlations of fat thickness have been generally reported as moderate in magnitude with other carcass traits. Phenotypic correlations of fat thickness with carcass weight were between 0.24 and 0.42

(Koch, 1978; Koch et al. 1982; Lamb et al. 1990; Wilson et al. 1993). Fat thickness has been reported by most researchers to have a positive genetic correlation with marbling score. However, Wilson et al. (1993) estimated this correlation to be -0.13. Koch (1978), Koch et al. (1982) and Lamb et al. (1990) found this genetic correlation to be moderate and positive, ranging in magnitude from 0.16 to 0.73. The phenotypic correlations reported in the literature between fat thickness and marbling score were positive, ranging from 0.12 to 0.25 (Koch, 1978; Koch et al. 1982; Lamb et al. 1990; Wilson et al. 1993). Arnold et al. (1991) reported that reduced fat thickness was associated with larger ribeye area (Rg = -0.37) and reduced marbling (Rg = -0.19). Koch et al. (1982) reported that the genetic correlation between fat thickness and estimated cutability (yield grade) was -0.74. This is expected since increased fat reduces estimated lean yield in the carcass. Fat thickness had the highest genetic correlation with fat trim (Rg = 0.95) in the study of Koch (1978). Koch (1982) also found a positive genetic correlation (Rg = 0.26) between fat thickness and Warner-Bratzler shear force, indicating an unfavorable relationship between fat thickness and tenderness. The corresponding phenotypic correlation reported by Koch et al. (1982) between fat thickness and Warner-Bratzler shear force was near zero (Rp = -0.01).

Carcass yield, measured as expected percent by USDA yield grade, or in actual retail product yield (total lean yield) has been reported in the literature to have strong associations with hot carcass weight and fat thickness. The

genetic correlations of yield with hot carcass weight ranged from 0.45 to 0.90 in the reports of Koch (1978) and Koch et al. (1982). The genetic correlations of yield with fat thickness were generally negative in these studies.

Phenotypic correlations reported for marbling score were positive with hot carcass weight, near zero for longissimus muscle area and moderately positive with fat thickness. The genetic correlations of marbling score with estimated cutability or retail product percent were negative, ranging in value from -0.12 to -0.37. Marbling score was also reported to have negative genetic correlations with Warner-Bratzler shear force (Koch et al. 1982; Van Vleck et al. 1992). Similarly, Van Vleck et al. (1992) reported a positive genetic correlation (Rp = 0.74) with sensory panel tenderness. These results indicate that a favorable relationship exists between marbling score and tenderness. Marshall (1994) stated that, after reviewing several studies reported in the recent literature, marbling seemed to have a positive, though relatively weak, relationship with palatability, and the relationship tends to be a topic of much debate. Marshall (1994) further stated that genetic correlations in the literature indicate, at least in some populations, that selection for increased marbling might be antagonistic to selection for improved cutability and perhaps increased muscling. He also summarized that based on across-study averages, genetic correlations indicated a possible selection antagonism between increased muscling and decreased fat thickness.

Tenderness, measured with trained sensory panels, or by Warner-Bratzler shear force, had favorable or near zero phenotypic and genetic correlations with other carcass traits. Phenotypic correlations of Warner-Bratzler shear force with other carcass traits were generally near zero. However, Koch et al. (1982) and Van Vleck et al. (1992) found phenotypic correlations of Warner-Bratzler shear force with marbling score to be -0.12 and -0.18, respectively. Van Vleck et al. (1992) also reported a negative genetic correlation of Warner-Bratzler shear force with sensory panel tenderness of -0.96. Shackelford et al. (1994) reported that the genetic correlation of calpastatin activity with Warner-Bratzler shear force was 0.59, indicating a strong genetic relationship between the activity of proteolytic inhibition and tenderness. Warner-Bratzler shear force was also reported to have negative (favorable) genetic correlations with ribeye area and marbling score (Koch et al. 1982; Van Vleck et al. 1992), estimated retail yield (Koch et al. (1982) and retail product weight (Koch et al. 1982; Shackelford et al. 1994). However, unfavorable genetic correlations (positive) were found to exist between Warner-Bratzler shear force and fat thickness, fat trim weight and fat trim percent (Koch et al. 1982).

In summary, it has been reported in the literature that direct and maternal additive effects of Brahman influence reduce carcass weight, marbling score and tenderness when compared to the corresponding effects of *Bos taurus* breeds. The variation in tenderness, measured by Warner-

Bratzler shear force or trained sensory panels, merits further investigation. Direct and maternal Angus and Hereford effects were similar for carcass composition traits, but the direct additive effect of Angus was often reported to be higher for marbling score than other breed types. The direct and maternal additive effects of Charolais has been reported to increase weight of the carcass and total lean yield. Generally, direct heterosis has been shown to increase hot carcass weight, fat thickness and marbling score, but maternal heterosis has been reported to have smaller effects on carcass traits.

Genetic parameters among carcass traits have been widely studied in the literature, however, there is a need for genetic parameter estimation in populations of Brahman influenced beef cattle. Most researchers have characterized the heritabilities of carcass traits to be moderate to high, indicating that selection would be possible. Positive genetic associations have been reported between increased growth rate and weight and tenderness; however, some studies have indicated that there may be a selection antagonism between increased weight and marbling score. Genetic correlations between early-life traits and carcass traits have not been sufficiently studied. Phenotypic and genetic associations between carcass traits and traits of economic importance to earlier phases of the beef cycle must be estimated before sound selection decisions can be made.

CHAPTER 3

GENETIC PARAMETERS FOR FEEDLOT PERFORMANCE, CARCASS COMPOSITION AND MEAT QUALITY TRAITS AMONG BRAHMAN-INFLUENCED BEEF STEERS ESTIMATED USING A MULTIVARIATE MIXED SIRE MODEL (PHASE I)

Introduction

Traits associated with postweaning growth performance, carcass composition and meat quality have received greater attention in the recent scientific literature. Crossbreeding is a widely used system for production of beef cattle. Review articles by Cundiff (1970), Franke (1980), Gregory and Cundiff (1980), Long (1980) and Turner (1980) have indicated that crossbreeding is an effective tool to make use of additive and non-additive genetic variation among breeds. Carcass traits including yield and palatability are important in the evaluation of breeds and breed combinations for beef production. In the Gulf Coast Region of the United States beef industry, the use of *Bos indicus* genetic resources is widespread. Numerous researchers (Carpenter, 1962; Peacock et al., 1978; Crouse et al., 1989, Huffman et al., 1990, DeRouen et al., 1992) have reviewed differences among *Bos indicus* and *Bos taurus* breeds and their crosses and reported that measures of beef quality, including marbling and tenderness, tend to decrease with increasing fractions of *Bos indicus* inheritance. The continued importance of *Bos indicus*, especially Brahman, genetics in the U.S. beef cow herd warrants further investigation of the effects of Brahman inheritance on carcass composition and

meat quality. The widespread use of Brahman genetics is often complemented by crossbreeding using a diverse range of breeds of *Bos taurus* origin, including the Bristish and Continental European breeds. Comparisons among representative breeds of these types under similar environmental and production systems are needed. Additive and non-additive maternal and direct breed effects have a significant impact on carcass composition or meat quality traits (Gregory et al., 1978; Peacock et al., 1982; Koch et al., 1983). Consideration of direct and maternal additive and non-additive breed effects is important in the design of efficient crossbreeding programs.

Mixed model procedures for genetic evaluation of beef cattle have become widely accepted as a selection tool by both purebred and commercial beef producers. Genetic comparisons between breeds will be valuable in the development of breeding objectives and strategies for mulitple-breed management systems (Arnold et al., 1992). Further, estimates of genetic parameters are needed. Although sire summaries are published by national breed associations, few of these incorporate genetic evaluation of postweaning growth or carcass traits. As the importance of postweaning performance, carcass composition and meat quality continues to increase, estimation of genetic parameters for these traits under diverse environments and production systems will become more important.

Wilson et al. (1992) and Crews (1995) have pointed out that equitable evaluation of carcass merit is complicated by lack of uniformity in feeding end

point. Further, the executive summary of the National Beef Quality Audit (NCA, 1992) attributed nearly $250 of lost profit potential due to genetic mismanagement or non-conformity. An overall goal of the genetic evaluation of carcass traits should be to identify, and remove from the population, cattle which do not have the genetic ability to produce desirable carcasses under present industry standards.

The objectives of the present study were to evaluate feedlot performance, carcass composition and meat quality among straightbred and crossbred steer progeny from five breeds: Angus, Brahman, Brangus, Charolais and Hereford; to estimate genetic parameters for these traits; and to estimate direct and maternal additive and non-additive breed effects for feedlot performance and carcass traits under a similar management system in the subtropical Southern U.S.

Materials and Methods

Data Collection and Cattle Management. The data for these analyses consisted of records from steers (N = 708) born from 1960 to 1968 at the LSU Ben Hur Crossbred Beef Cattle Research Unit. The climate is characterized as subtropical, with average daily minimum and maximum temperatures of 13 and 26° C, average daily minimum and maximum humidity of 54 and 88% and an average annual rainfall of 147 cm. Sires representing five breeds were used: Angus, Brahman, Brangus, Charolais and Hereford. Calves were produced from a crossbred mating design that included the

production of straightbreds, first (F_1) crosses, three-breed- and back-crosses, and 2- and 3-breed rotational crosses.

Calves were born during spring calving seasons and bull calves were castrated at birth. Only steers were fed and slaughtered, therefore the data consisted of steer records. Preweaning management practices were followed and calves were weaned at approximately 8 mo of age. The steers were then full fed under feedlot conditions for 168 d on a high energy corn-based diet. At the completion of the feeding period, steers were slaughtered and carcass traits were measured. Feedlot performance data were: weight at the begining of the feeding period (WTONF), feedlot daily gain (FDG) and slaughter weight (SWT). Carcass traits measured included hot carcass weight (HCW), adjusted fat thickness over the longissimus muscle at the 12-13th rib interface (FAT), area of the longissimus (ribeye) muscle (REA), carcass weight adjusted ribeye area (WAR), percentage of carcass weight as fat in the kidney, pelvic and heart (KPH) regions, USDA marbling score (MAR) and Warner-Bratzler shear force (WBS). Warner-Bratzler shear force is an objective measure of tenderness, taken as the force required to shear a 2.54 cm core from a cooked steak from the longissimus muscle. The data set was edited to remove all records with missing data. The steers in this data represented breeds that were popular in the beef industry in the Southern Region during the period of 1960 to 1968, but would be considered different biological types than steers of similar breeding in the current industry.

Data Analyses. Data were analyzed using the REMLPK (Restricted Maximum Likelihood with Canonical Transformation) programs of Meyer (1985), the MTDFREML (Multiple Trait Derivative Free Restricted Maximum Likelihood) programs of Boldman et al. (1995) and general linear model procedures of the SAS system (SAS, 1989). REMLPK is a set of programs for the univariate or multivariate analysis of data with two random (e.g., sire and residual) effects in a mixed model. The programs perform a canonical decomposition to reduce the data from multivariate to a series of univariate analyses, with an expectation-maximization (EM) type algorithm with tridiagonalization of the coefficient matrix of the mixed model equations. REMLPK allows for the fitting of a mixed sire model, with the restrictions that data must have no missing records, and that the model only include a single random effect (sire) other than the residual term. MTDFREML is a set of programs to obtain estimates of (co)variance components using mixed models and derivative-free restricted maximum likelihood (DFREML) estimation. In this analysis, REMLPK was used to obtain estimates of (co)variance components with accompanying standard errors and MTDFREML was used to obtain estimates and contrasts of covariates and fixed effects. The general form of the mixed (sire) model used in this analysis is:

$$y = X\beta + Zu + e$$

where

y = a vector of Nt observations of t traits measured on n_i progeny of sire i,

X = a known incidence matrix relating observations to fixed effects,

Z = a known incidence matrix relating observations to random effects,

β = a vector of unknown fixed effects,

u = a vector of unknown random (sire) effects, and

e = a vector of unknown random residual effects not explained by Xβ and Zu.

The mixed model equations (MME) are of the form

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z+G^{-1} \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{u} \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}$$

$$E \begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} X\beta \\ 0 \\ 0 \end{bmatrix}$$

$$var \begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} V & ZG & R \\ GZ' & G & 0 \\ R & 0 & R \end{bmatrix}$$

The following distributional assumptions were made in using the mixed sire model: V = var (y) = Z G Z' + R with order equal to the number of progeny records times the number of traits and G = var (u) = A ⊗ G_0 , with G_0 being

a t by t matrix of genetic (co)variances of sire effects (one-fourth the additive genetic (co)variance matrix) for the t traits in the analysis and A the numerator relationship matrix for sires. The inverse of G, $G^{-1} = A^{-1} \otimes G_0^{-1}$ is computed according to the rules of Henderson and Quaas (1976). Finally, R is the residual (co)variance matrix, where $R = \text{diag}\{ R_i \}$, $i = 1, ..., N$, where R_i is a t by t matrix of residual (co)variances for progeny i. Priors for the genetic and residual (co)variances in G_0 and R_0 were supplied from recent estimates reported in the scientific literature. The estimates of the β and u were shown by Henderson (1959; 1963) to be best linear unbiased estimates (BLUE) and best linear unbiased predictors (BLUP), respectively. Covariates in the model included direct additive breed fractions (as a percentage of each breed of sire), maternal additive breed fractions (direct additive breed fractions for the dam), total direct heterosis (percentage of total direct breed heterozygosity in the steer), total maternal heterosis (percentage of total direct breed heterozygosity in the dam), julian birth date within calving season (d), age of dam (yr) and slaughter age (d). Year of birth was included as a fixed effect. The direct and maternal additive and non-additive breed fractions used as covariates were generated using CANAGE, a set of programs to obtain direct and maternal additive and heterosis fractions for crossbred data (Gould and Crews, 1996). The total direct and total maternal heterosis fractions were calculated as the sum of all possible non-additive unlike breed combinations. With respect to direct and maternal additive breed fraction covariates, the solution for the

Brahman covariates (direct and maternal) were constrained to zero in order to maintain full rank in the coefficient matrix of the mixed model equations. All traits were simultaneously fit with the model, and convergence (defined as when estimates of random effects changed less than .0001 % from one iteration to the next) was attained after approximately twenty thousand rounds of iteration. The solutions for sire components of (co)variances were multiplied by a factor of four to obtain corresponding estimates of additive genetic components of (co)variance. Fixed effect solutions of interest included contrasts of direct and maternal additive breed effects, Brahman versus non-Brahman direct and maternal breed effects and solutions for direct and maternal heterosis. Estimates of additive genetic and phenotypic (co)variances were then used to calculate heritabilities and genetic and phenotypic correlations among traits. The mixed model equations included 1079 animals from 44 sires in the numerator relationship matrix.

Results and Discussion

A summary of model information including number of steers within each sire breed and summary statistics for fixed effects and covariates is presented in tables 3.1 and 3.2. Summary statistics for feedlot performance, carcass composition and meat quality traits are also given in table 3.2.

Genetic Effects. Weight at the beginning of the feedlot period (WTONF) was assumed to be similar to weight at weaning. Numerous researchers have shown that significantly large maternal effects and heterosis levels affect the

Table 3.1 Numbers of Steers Represented in Each Sire Breed Group.

	Angus	Brahman	Brangus	Charolais	Hereford
N progeny	150	131	155	127	145

Table 3.2 Sample Summary Statistics for Response Variables.

Trait	MIN	MAX	AVG	STD
WTONF, kg	83.915	294.838	202.661	34.199
FDG, kg/d	0.2449	1.4697	0.8392	0.1760
SWT, kg	207.747	544.316	362.056	49.4461
HCW, kg	151.80	353.806	220.394	35.3811
FAT, cm	0.127	12.1667	1.6805	1.0339
REA cm^2	12.261	90.328	59.4695	7.9833
WAR, cm^2	0.9309	1.9896	1.3099	0.1758
KPH, %	0.300	9.000	3.0483	1.0052
MAR	1.000	17.000	7.8501	3.2870
WBS, kg	5.3978	23.587	10.9285	3.1707

Table 3.3 Estimates of Direct Additive Genetic Effect Contrasts (s.e.) for Feedlot Performance Traits.

Contrast	WTONF	FDG	SWT
A - B	-35.13* (9.35)	-0.015 (.060)	-34.06* (14.44)
A - BR	-15.75* (7.64)	-0.033 (.051)	-19.47 (12.42)
A - C	-39.34* (8.94)	-0.106 (.058)	-57.74* (14.16)
A - H	-17.27 (9.10)	-0.141* (.058)	-25.99 (14.08)
B - BR	19.38* (9.31)	-0.018 (.060)	14.59 (14.49)
B - C	-4.21 (9.89)	-0.091 (.064)	-23.68 (15.38)
B - H	17.87* (8.84)	-0.127* (.057)	8.07 (13.86)
BR - C	-23.59* (8.91)	-0.073 (.059)	-38.26* (14.27)
BR - H	-1.52 (9.06)	-0.109 (.058)	-6.52 (14.09)
C - H	22.08* (9.61)	-0.036 (.062)	31.75* (14.91)
B(DIR)	17.04* (7.60)	-0.052 (.049)	8.26 (11.75)

* $P < .05$.

expression of early-life weight traits, however, for purposes of uniformity in the model, and due to restraints of the REMLPK software, only additive effects due to sires were fit in this model. Table 3.3 contains direct additive genetic effect contrasts for feedlot performance traits. Individual breed effects solutions can be found for each breed by inspection of the appropriate contrast with the Brahman. The Brahman solution for additive and maternal direct effects were set to zero for all analyses. As such, only the contrasts will be reported, not the breed effects solutions. The contrasts of all pairwise direct additive breed effects show that the Angus effect was smaller than that of all other breeds. In the study of Urick et al. (1991), researchers found that when Angus was the maternal breed of sire, all postweaning weights were smaller than when the maternal breed of sire was Simmental, Pinzgauer or Tarentaise. The solution for the Angus effect was from 15.75 to 39.34 kg smaller than that for Brahman, Brangus, Charolais and Hereford. Among steers of known percentage Angus and Brahman breeding, Huffman et al. (1990) reported that straightbred and 3/4 Angus steers had lighter initial feedlot weights that 1/2- and 3/4-Brahman steers. Conversely, the solution for the Brahman direct additive effect was larger than that for Angus (35.13 kg), Brangus (19.38 kg) and Hereford (17.87 kg). Angus-sired steers out of Hereford dams were intermediate and similar to steers sired by Pinzgauer, Tarentaise, Simmental and Red Poll bulls. The Brahman versus Charolais effect contrast of 4.21 kg in favor of the Charolais, was not significant ($P > .05$). The Brangus effect

was smaller than that of Charolais (-23.59 kg), but was not different from that of Hereford. The ranking of the five direct additive breed effects for WTONF implied from these contrasts was: Charolais, Brahman, Hereford, Brangus, Angus. The contrast of Brahman versus non-Brahman genetic effects showed an advantage ($P < .05$) for the Brahman effect of approximately 17 kg. Previous studies have shown an advantage of Brahman influence in weight traits near weaning. Huffman et al. (1990) showed that increasing Brahman influence from zero to 75 % generally resulted in increased initial feedlot weight.

The direct additive effect contrasts for feedlot daily gain (FDG) are also shown in table 3.3. The Angus effect tended to be smaller than that of Brahman, Brangus and Charolais (-0.015, -0.033 and -0.106, respectively) but these contrasts were not significant ($P > .05$). The Angus effect was lower for FDG than the Hereford ($P < .05$) Likewise, Brahman effects tended to be smaller for gain per day on feed than Brangus and Charolais effects, but the differences were not significant. The additive genetic effect of Hereford was about 0.127 kg larger per day on feed than was the Brahman effect ($P < .05$). The contrasts of Brangus with Charolais and Hereford tended to be negative, but were not significant. Likewise, the contrast of Charolais versus Hereford additive effects was negative, but not significant in these data. The contrast of Brahman versus non-Brahman was also negative (-0.052) indicating a tendency for higher FDG due to the non-Brahman genetic effect, but the

difference was not significant (P > .05). Huffman et al. (1990) showed that increased Brahman influence was associated with increased average daily gain on feed.

The direct additive breed contrasts for slaughter weight (SWT) (table 3.3) showed the Angus effect to be smaller than Brahman and Charolais effects, but similar (P > .05) to Brangus and Hereford effects. The direct additive effects of Brahman tended to be similar for SWT to the Brangus, Charolais and Hereford effects. The effect of Brangus was approximately 38.26 kg smaller (P < .05) than that of Charolais, but was not different than the Hereford effect. The Charolais effect was the heaviest for slaughter weight, although not significantly moreso than the Brahman effect. Finally, the difference in additive genetic effects on SWT between Brahman and non-Brahman (8.26 kg) was not significant (P > .05). These results show that weight differences at or near weaning tended to diminish during the feeding period. The Charolais effect tended to be heavier for both beginning and ending feedlot weights, but did not differ for FDG from other additive genetic breed effects. The contrasts of Brahman versus non-Brahman showed that the increase in weight due to the direct additive effect of Brahman at the beginning of the feedlot period became smaller at the end of the feedlot period when compared to the average non-Brahman effect. The results of Huffman et al. (1990) indicated that the range of initial and final feedlot weight were similar among steers of varying percentages of Brahman and Angus breeding.

The direct heterosis effect was significantly positive and different from zero for WTOF and SWT, but near zero for FDG (table 3.4). The total direct heterosis solution for SWT was 23.50 kg, indicating that significant advantages due to non-additive genetic action were present throughout the feedlot phase.

Contrasts among maternal additive breed effects for feedlot performance traits are given in table 3.5. The contrasts involving Angus as a maternal additive breed effect indicate that the maternal additive Angus effect for WTOF was larger than that of the Hereford, smaller than that of the Charolais and not different from that of Brahman and Brangus. Brahman and Brangus maternal additive effects were similar, but again the Brahman maternal additive effect was smaller (18.46 kg) than that of Charolais with respect to WTOF. The maternal additive effect of Brangus tended to be smaller than that of Charolais (10 kg), but was not significant. The Brangus maternal additive effect was 22.13 kg larger than that of Hereford. Lastly, the Hereford maternal additive effect was approximately 32 kg smaller than that of Charolais, indicating that the maternal additive effect of the Charolais was largest, and significantly larger than that of other breeds.

The maternal additive effects on FDG were mostly not significant ($P > .05$) with the exception that the maternal additive effect for Angus was 0.098 kg/d larger ($P < .05$) than that for Brahman. The contrast of Brahman versus non-Brahman maternal additive effect on FDG was negative (-0.072 kg/d)

Table 3.4 Estimates of Direct and Maternal Heterosis Effects (s.e.) for Feedlot Performance, Carcass Composition and Meat Quality Traits.

Trait	Total direct heterosis	Total maternal heterosis
WTONF	0.783* (.28)	-0.741* (.05)
FDG	-0.002 (.002)	0.001* (.000)
SWT	23.51* (4.24)	13.26* (3.37)
HCW	18.51* (3.08)	9.24* (2.41)
FAT	0.227* (.107)	-0.101 (.084)
REA	2.02* (.75)	9.65* (.60)
WAR	0.045* (.017)	0.021 (.013)
KPH	0.394* (.099)	0.144 (.078)
MAR	0.599 (.77)	0.174 (.23)
WBS	-0.606* (.296)	0.056 (.228)

* $P < .05$.

Table 3.5 Estimates of Maternal Additive Genetic Effect Contrasts (s.e.) for Feedlot Performance Traits.

Contrast	WTONF	FDG	SWT
A - B	-1.45	0.098*	22.71*
	(5.93)	(.039)	(9.50)
A - BR	-9.91	0.022	-6.76
	(5.24)	(.035)	(8.70)
A - C	-19.91*	0.057	0.18
	(7.50)	(.051)	(12.51)
A - H	12.22*	0.024	8.95
	(5.81)	(.038)	(9.33)
B - BR	-8.46	-0.077*	-29.47*
	(6.01)	(.040)	(9.66)
B - C	-18.46*	-0.041	-22.53
	(7.87)	(.053)	(12.98)
B - H	13.67*	-0.074	-13.76
	(5.76)	(.038)	(9.38)
BR - C	-10.00	0.036	6.94
	(7.54)	(.051)	(12.61)
B - H	22.13*	0.003	15.71
	(5.79)	(.038)	(9.32)
C - H	32.13*	-0.033	8.78
	(7.62)	(.051)	(12.63)
B (MAT)	-2.95	-0.072*	-22.12*
	(4.99)	(.033)	(8.04)

* $P < .05$.

indicating that the maternal Brahman genetic effect negatively influenced feedlot daily gain relative to the average non-Brahman maternal effect.

With regard to slaughter weight (SWT), the maternal additive genetic effects of the four breeds were generally similar. The Brangus and Angus maternal additive effects on slaughter weight were 29.47 and 22.71 kg larger ($P < .05$) than that of the Brahman. Similarly, the maternal additive effect of Brahman was 22.12 kg smaller ($P < .05$) than that of non-Brahman.

Genetic Parameters. Sire genetic, residual and phenotypic variances for feedlot traits are given in table 3.6. The estimates of additive genetic variance, taken to be four times the estimate of the sire component of variance from the REMLPK programs, were 27.53, 0.0042 and 167.11 kg^2 for WTOF, FDG and SWT, respectively. Likewise, the phenotypic variance estimates for these traits were 487.41, 0.0254 and 1502.86 kg^2, respectively. The heritability estimates for these traits (table 3.7) were moderate to high. The heritabilities ($\pm$ standard error) for weight on feed, feedlot daily gain and slaughter weight were 0.226 $\pm$ .027, 0.663 $\pm$ .046 and 0.445 $\pm$ .038, respectively. Sire genetic and phenotypic covariances are given in table 3.8. These results are similar to those of Reynolds et al. (1991) who reported heritabilities of 0.50 for gain and 0.49 for slaughter weight based on son-sire covariances in a herd of non-selected Herefords. The heritability of eight to twelve month weight among Hereford bulls and heifers in the study of DeNise and Torabi (1989) was 0.41. They reported the heritability of 12- to 20-

Table 3.6 Estimates of Sire Genetic, Residual and Phenotypic Variances (s.e.) for Feedlot Performance Traits.

Trait	Sire Genetic Variance	Residual Variance	Phenotypic Variance
WTONF	27.5252 (13.819)	459.888 (25.415)	487.4137 (27.544)
FDG	0.00422 (.00137)	0.02122 (.01177)	0.02544 (.00175)
SWT	167.1141 (62.606)	1335.748 (74.009)	1502.862 (92.783)

Table 3.7 Estimates of Heritabilities (h^2), Genetic (Rg) and Phenotypic (Rp) Correlations (s.e.) for Feedlot Performance Traits[a].

Trait	WTONF	FDG	SWT
WTONF	0.226 (.027)	0.159 (.042)	0.652 (.023)
FDG	0.662 (.212)	0.663 (.046)	0.756 (.019)
SWT	0.781 (.1369)	0.908 (.057)	0.445 (.038)

a Heritabilities are on the diagonal, genetic correlations are below the diagonal and phenotypic correlations are above the diagonal.

month gain was 0.24. Twelve month weight had a heritability of 0.41 in the data of DeNise and Torabi (1989).

As expected, feedlot performance traits had high levels of genetic association, as shown by the additive genetic correlations given in table 3.7. These correlations ranged from Rg = 0.662 between weight on feed and feedlot daily gain to Rg = 0.908 between feedlot daily gain and slaughter weight. Gain on test had a genetic correlation of 0.98 with slaughter weight in the study of Reynolds et al. (1991). DeNise and Torabi (1991) reported a genetic correlation of 0.67 between 8- to 12-month gain and 12- to 20-month gain among Hereford bulls. The genetic correlation between weight on feed and slaughter weight was intermediate (Rg = 0.781) but significantly large. Other researchers have reported high genetic correlations between weights at the beginning and end of feeding (DeNise and Torabi, 1989; Reynolds et al., 1991). Similarly, phenotypic correlations among feedlot performance traits were high, with the exception of that between weight on feed and feedlot daily gain (Rp = 0.159) which was significantly different from zero, but not as large as those between feedlot daily gain and slaughter weight (Rp = 0.756) or between weight on feed and slaughter weight (Rp = 0.652).

Carcass Composition and Meat Quality Traits. Direct additive breed effect contrasts for carcass composition traits are given in table 3.9. The Brahman direct additive effect for hot carcass weight (HCW) was 22.47 kg larger than that of Angus. Huffman et al. (1992) noted an increasing trend in

Table 3.8 Estimates of Sire Genetic and Phenotypic Covariances (s.e.) for Feedlot Performance Traits[a].

Trait	WTONF	FDG	SWT
WTONF		0.5581 (.1564)	558.217 (42.549)
FDG	0.2254 (.1069)		4.6750 (.3623)
SLWT	52.943 (25.616)	0.7621 (.2728)	

a Genetic covariances are in the lower triangle, phenotypic covariances are in the lower triangle.

Table 3.9 Estimates of Direct Additive Genetic Effect Contrasts (s.e.) for Carcass Composition Traits.

Contrast	HCW	FAT	REA	WAR	KPH
A - B	-22.47*	0.744*	0.254	0.006	1.32*
	(9.63)	(.32)	(2.56)	(.06)	(.33)
A - BR	-2.41	0.762*	2.149	0.047	0.96*
	(8.53)	(.29)	(2.20)	(.049)	(.28)
A - C	-31.40*	1.220*	-16.09*	-0.354*	1.82*
	(9.59)	(.32)	(2.51)	(.055)	(.32)
A - H	-13.14	0.647*	-0.883	-0.019	1.01*
	(9.39)	(.32)	(2.50)	(.055)	(.32)
B - BR	20.06*	0.015	1.896	0.042	-0.37
	(9.68)	(.33)	(2.57)	(.057)	(.33)
B - C	-8.92	0.478	-16.35*	-0.360*	0.49
	(10.29)	(.35)	(2.73)	(.061)	(.35)
B - H	9.33	-0.097	-1.14	-0.025	-0.31
	(9.34)	(.32)	(2.46)	(.054)	(.31)
BR - C	-28.98*	0.460	-18.24*	-0.402*	0.86*
	(9.71)	(.33)	(2.53)	(.056)	(.33)
BR - H	-10.73	-0.115	-3.033	-0.067	0.05
	(9.41)	(.32)	(2.50)	(.055)	(.32)
C - H	18.25	-0.575	15.21*	0.335*	-0.81*
	(9.95)	(.34)	(2.64)	(.058)	(.34)
B(DIR)	10.73	-0.086	-3.959	-0.087	-0.38
	(7.84)	(.26)	(2.08)	(.046)	(.27)

* $P < .05$.

HCW of steers with increases in Brahman versus Angus breeding. The Charolais effect on HCW was larger than the Angus and Brangus effects, but was similar to those of the Brahman and Hereford. Peacock et al. (1979) also found that Charolais-sired steers had heavier carcass weights than Angus-sired steers. DeRouen et al. (1992) found that among straightbreds, Charolais had heavier carcass weights than Angus, Brahman and Hereford. The Brangus effect increased HCW by 20 kg compared to the Brahman effect. All other direct additive breed contrasts were not significant ($P > .05$). DeRouen et al. (1992) also found that Angus and Hereford were similar for HCW. This was also in general agreement with other researchers who reported similar HCW for Angus and Hereford (Urick et al., 1974; Bertrand et al., 1983; Baker et al., 1984). The Brahman versus non-Brahman direct additive contrast tended to be positive in favor of the Brahman genetic effect, but was not significantly different from zero. DeRouen et al. (1992) also found that Brahman and Hereford straighbtred steers had similar HCW. Comerford et al. (1988) found that Brahman carcasses were lighter ($P < .01$) than the average of Simmental Limousin and Hereford carcasses. Peacock et al. (1979) reported that Charolais steers were superior for growth, carcass weight and yield compared with Angus and Brahman steers.

All direct additive contrasts involving the Brahman, Brangus, Charolais and Hereford for fat thickness at the 12th rib interface were not significant ($P > .05$). However, the Angus effect was from 0.65 to 1.22 cm larger for FAT

than all other effects. This was in agreement with the findings of Urick et al. (1991) who reported that Angus-sired steers had more fat cover at the 12th rib than did steers sired by Tarentaise, Red Poll, Simmental or Pinzgauer bulls. Sanders and Paschal (1987) reported that Angus-sired steers were fatter than zebu- and Senepol-sired steers. The contrast of Brahman versus non-Brahman direct additive effects on fat thickness was near zero (-0.086 cm). This was proabably due in part to the direct additive Angus contribution to the average non-Brahman effect, and the similarity among additive genetic effects on fat thickness of Brangus, Hereford and Charolais.

Similar to fat thickness, few significant direct additive breed differences were detected for ribeye area. The Charolais effect increased ribeye area from 15.21 to 18.24 cm^2 compared to the other genetic effects, but all contrasts not involving the Charolais were not significant. Peacock et al. (1979) also reported that steers with Charolais breeding had larger ribeye area than those with Angus and Brahman breeding. Similar results were found with respect to carcass-weight adjusted ribeye area. Since an increase in ribeye area is expected with increases in hot carcass weight, this measure has been suggested as a better indicator of carcass muscling than simple ribeye area; however, in these data, the Charolais effect was from 0.335 to 0.402 cm^2 larger for ribeye area per unit carcass weight than the other genetic effects. The contrasts of carcass-weight adjusted ribeye area among the Angus, Brahman, Brangus and Hereford genetic effects were not significant.

Percent of carcass weight as kidney, pelvic and heart fat was similar among all direct additive genetic effects except the Angus, which was larger for KPH fat than the Brahman, Brangus, Charolais and Hereford (0.957 to 1.817%) effects. Also, the Charolais effect on KPH was smaller than the Brangus and Hereford effects. Reports in the literature for breed effects on KPH are conflicting. Huffman et al. (1992) found no differences in KPH among steers with zero to 75 % Brahman or Angus breeding.

With regard to marbling score, the Angus had a higher direct additive genetic effect for marbling score than all other breeds evaluated except the Hereford (table 3.10). The Hereford was next in marbling score to Angus, but reduced scores 3.14 units compared to the effect of Angus. In contrast to the Angus, the marbling score contrasts involving the additive effects of Brahman were significantly ($P < .05$) negative in all cases except versus the Charolais effect, which indicated that the direct additive effect on marbling score of Brahman and Charolais were similar. Contrasts revealed that the Brahman effect reduced marbling scores from 3.22 (versus the Brangus effect) to 6.36 (versus the Angus effect) compared to the other direct additive effects. The Brangus effect on marbling score was higher than the Angus, Brahman and Charolais effects but was similar to that of Hereford. The direct additive effect of Charolais on marbling score was lower likewise than the Angus, Brangus and Hereford effects, but was similar to the effect of Brahman. The contrast of direct additive breed effects of Brahman versus non-Brahman indicated that

Table 3.10 Estimates of Direct Additive Genetic Effect Contrasts (s.e.) for Meat Quality Traits.

Contrast	MAR	WBS
A - B	6.36* (.95)	-4.16* (.82)
A - BR	3.14* (.83)	-1.13 (.75)
A - C	5.46* (.94)	-0.65 (.83)
A - H	1.58 (.93)	-1.77* (.80)
B - BR	-3.22* (.95)	3.03* (.83)
B - C	-0.90 (1.01)	3.51* (.88)
B - H	-4.78* (.92)	2.39* (.81)
BR - C	2.32* (.95)	0.48 (.84)
BR - H	-1.56* (.93)	-0.64 (.80)
C - H	-3.88* (.98)	-1.12 (.85)
B (DIR)	-3.82* (.77)	3.27* (.67)

* $P < .05$.

the Brahman genetic effect resulted in a reduction ($P < .05$) in marbling score by 3.82 units compared to the average non-Brahman effect. Most researchers have reported lower marbling scores among Brahman when compared to non-Brahman contemporaries (Peacock et al., 1979; Huffman et al., 1990). Numerous reviews of breed and genetic effects on marbling score have been given (Crews, 1992; 1996). Huffman et al. (1992) showed a reduction in percent US Choice quality grades with increases in percentage Brahman breeding. Similarly, Carpenter et al. (1961) showed a linear decrease in marbling score with increases in Brahman (versus Shorthorn) influence.

Tenderness, measured as the force required to shear a 2.54 cm core of from a cooked steak from the longissimus, was not different among Angus, Brangus and Charolais direct additive effects (table 3.10). All contrasts involving Brahman, however, showed the Brahman effect to increase ($P < .05$) Warner-Bratzler shear force values compared to the additive genetic effects of other breeds evaluated. In addition to lowered marbling score, numerous researchers have reported higher Warner-Bratzler shear force, thus lower tenderness, in Brahman as compared to non-Brahman. The contrast of Brahman versus non-Brahman additive genetic effects in these data showed a 3.27 kg advantage for the non-Brahman effect with regard to Warner-Bratzler shear force.

The maternal additive breed effects on carcass traits (table 3.11) were not as large as direct additive breed effects. Angus and Charolais had similar

Table 3.11 Estimates of Maternal Additive Genetic Effect Contrasts (s.e.) for Carcass Composition Traits.

Contrast	HCW	FAT	REA	WAR	KPH
A - B	12.27 (6.54)	0.098 (.22)	0.55 (1.68)	0.012 (.037)	-0.353 (.22)
A - BR	-10.60 (6.12)	-0.137 (.21)	-4.17* (1.54)	-0.092* (.034)	-0.632* (.20)
A - C	-9.87 (8.86)	0.236 (.31)	2.89 (2.21)	0.064 (.049)	-0.628* (.29)
A - H	3.78 (6.44)	-0.115 (.22)	0.64 (1.65)	0.014 (.036)	-0.380 (.21)
B - BR	-22.88* (6.66)	-0.235 (.23)	-4.71* (1.71)	-0.104* (.038)	-0.280 (.22)
B - C	-13.26 (9.14)	0.137 (.32)	2.35 (2.30)	0.052 (.051)	-0.275 (.29)
B - H	-8.49 (6.53)	-0.213 (.22)	0.10 (1.66)	0.002 (.037)	-0.027 (.22)
BR - C	9.61 (8.94)	0.373 (.31)	7.06* (2.23)	0.156* (.049)	0.005 (.29)
BR - H	14.38* (6.43)	0.023 (.22)	4.81* (1.65)	0.106* (.036)	0.253 (.21)
C - H	4.77 (8.92)	-0.350 (.31)	4.81* (1.65)	-0.050 (.049)	0.248 (.29)
B (MAT)	-14.23* (5.56)	-0.102 (.19)	-0.705 (1.42)	-0.016 (.031)	-0.057 (.18)

* $P < .05$.

maternal additive breed effects for HCW. The maternal Brangus effect on HCW was heavier than that of Brahman by 22.88 kg and 14.38 kg heavier than the Hereford. The maternal additive breed effect of Brahman on carcass weight was negative (-14.23 kg) when compared to that of non-Brahman. All contrasts of maternal additive breed effects for fat thickness were not significant.

With respect to ribeye area (REA), the maternal additive effect of Brangus was larger than the Angus, Hereford, Brahman and Charolais maternal additive effects. The maternal additive effect of Hereford was also smaller than that of the Charolais. The contrast of Brahman versus non-Brahman indicated that although the maternal additive effect of Brahman influence was negative (-0.705 cm^2), the value was not significant ($P > .05$). The maternal additive genetic effects on WAR followed a similar pattern to that of actual ribeye area. The maternal Brangus effect was greater than that of the Angus, Brahman, Charolais and Hereford, but all other maternal additive breed effects contrasts were not significant ($P > .05$). The contrast of Brahman versus non-Brahman maternal additive effects was close to zero.

Few significant differences were observed for maternal additive breed effects on kidney, pelvic and heart fat. The Angus generally had the highest percentages of KPH fat, but were only significantly fatter than the Brangus (0.632 %) and the Charolais (0.628 %) maternal effects.

Table 3.12 Estimates of Maternal Additive Genetic Effect Contrasts (s.e.) for Meat Quality Traits.

Contrast	MAR	WBS
A - B	0.577 (.64)	0.758 (.59)
A - BR	0.483 (.59)	0.432 (.56)
A - C	-0.094 (.86)	0.234 (.82)
A - H	0.402 (.63)	0.804 (.58)
B - BR	-0.075 (.65)	-0.326 (.59)
B - C	-0.651 (.89)	-0.524 (.85)
B - H	-0.156 (.64)	0.047 (.59)
BR - C	-0.576 (.86)	-0.198 (.83)
BR - H	-0.081 (.63)	0.373 (.58)
C - H	0.496 (.83)	0.571 (.83)
B (MAT)	-0.360 (.54)	-0.390 (.50)

Maternal additive breed effects were not significant for marbling score or Warner-Bratzler shear force (table 3.12). It was hypothesized that the Brahman versus non-Brahman maternal additive breed contrasts would show a negative impact of Brahman influence on marbling and tenderness, but the maternally Brahman-influenced steers had marbling scores only 0.360 units lower than non-Brahman. The same contrast for Warner-Bratzler shear force showed a slight advantage of maternal Brahman influence on Warner-Bratzler shear force, which differs from most reports currently in the literature, but the difference (0.390 kg) was not significantly different from zero ($P > .05$).

The effect of direct heterosis was found to be positive for all carcass composition traits ($P < .05$) (table 3.4). Direct heterosis decreased Warner-Bratzler shear force by 0.606 kg. Marbling score did show an increase with direct heterosis, but the 0.599 unit advantage due to heterosis was not significant. Hot carcass weight was increased 9.24 kg and ribeye area increased 9.65 cm^2 due to the effects of heterosis in the dam, but all other traits associated with carcass composition and meat quality were not significantly ($P > .05$) affected by maternal heterosis.

Genetic Parameters for Carcass Traits. Sire genetic, residual and phenotypic variances for carcass composition traits are given in table 3.13. Phenotypic and sire genetic covariances among carcass traits are given in table 3.14. The sire model used in these analyses resulted in heritability estimates from 0.321 to 0.376 for all carcass composition traits except KPH, which had

Table 3.13 Estimates of Sire Genetic, Residual and Phenotypic Variances (s.e.) for Carcass Composition Traits.

Trait	Sire genetic variance	Residual variance	Phenotypic variance
HCW	63.7527 (27.094)	715.0423 (39.5377)	778.795 (45.7067)
FAT	0.08855 (.0356)	0.8542 (.0473)	0.9427 (.0565)
REA	4.1314 (1.775)	47.4278 (2.625)	51.559 (3.019)
WAR	0.0020 (.0008)	0.02301 (.00127)	0.02501 (.00146)
KPH	0.1085 (.0383)	0.7180 (.0398)	0.8265 (.0530)

Table 3.14 Estimates of Sire Genetic and Phenotypic Covariances (s.e.) for Carcass Composition Traits[a].

Trait	HCW	FAT	REA	WAR	KPH
HCW		7.238 (1.170)	94.041 (9.268)	2.071 (.2040)	10.9173 (1.174)
FAT	0.24077 (.7053)		0.51966 (.2936)	0.01145 (.00647)	0.2302 (.0398)
REA	10.3705 (5.643)	0.1370 (.1802)		1.1357 (.0665)	0.6621 (.2822)
WAR	0.2284 (.1243)	0.00302 (.00396)	.09099 (.0391)		0.0146 (.00622)
KPH	0.3797 (.7441)	0.02253 (.0269)	-0.0739 (.1847)	-0.00163 (.0041)	

a Genetic covariances are in the lower triangle, phenotypic covariances are in the upper triangle.

Table 3.15 Estimates of Heritabilities (h^2), Genetic (Rg) and Phenotypic (Rp) Correlations for (s.e.) Carcass Composition Traits[a].

Trait	HCW	FAT	REA	WAR	KPH
HCW	0.327 (.033)	0.267 (.0392)	0.469 (.0320)	0.469 (.0320)	0.430 (.0365)
FAT	0.101 (.2879)	0.376 (.035)	0.075 (.0416)	0.075 (.0416)	0.261 (.0908)
REA	0.639 (.1937)	0.227 (.2831)	0.321 (.032)	1.00 (.000)	0.101 (.0429)
WAR	0.639 (.1937)	0.227 (.2831)	1.00 (.000)	0.321 (.032)	0.101 (.0429)
KPH	0.144 (.2656)	0.230 (.2520)	-0.110 (.2763)	-0.110 (.2763)	0.525 (.0413)

a Heritabilities are on the diagonal, genetic correlations are below the diagonal and phenotypic correlations are above the diagonal.

a heritability estimate of 0.525 (table 3.15). Moderate to high heritabilities have been reported for these traits by numerous researchers (Marshall, 1994). The heritability of HCW, estimated to be 0.327, was similar to the estimates reported by Lamb et al. (1990), Reynolds et al. (1991), Veseth et al. (1993) and Wilson et al. (1993). The heritability estimates for HCW reported by these researchers was from 0.31 to 0.38. Other studies, however, have reported heritabilities in the range of 0.44 to 0.68 (Koch, 1978; Koch et al., 1982; Benyshek, 1981; MacNeil et al., 1994). In the present data, the heritability of FAT was estimated to be 0.376 which was similar to the estimates of Koch et al. (1982), Lamb et al. (1990), Wilson et al. (1993) and Gregory et al. (1995) but smaller than those of Koch (1978) and MacNeil et al. (1991). The heritabilities reported for REA in the literature have been generally higher, although highly variable among studies, than in the present study (0.321), but few parameters have been reported for cattle produced during this time period. Marshall (1994) summarized six estimates of heritability for REA and found an average of 0.37 which was similar to the estimate in these data, but the range of estimates summarized by Marshall extended from a low of 0.01 to 0.60. It is likely that the genetic structure of the cattle population has changed over time, resulting in the differences shown here.

Genetic correlations showed that ribeye area and carcass weight adjusted ribeye area are essentially the same trait (Rg = 1.00). Although moderately large genetic correlations were found among carcass composition

traits, most of these correlations had standard errors too large to conclude that they were different from zero, possibly due to the relatively small size of the data set. Research has shown that positive genetic correlations exist among carcass composition traits associated with growth (hot carcass weight and ribeye area) and among carcass traits associated with fatness (fat thickness, marbling score and KPH fat) (Marshall, 1994). All phenotypic correlations among carcass composition traits were positive and low to moderate in magnitude. The dependency among carcass traits as evidenced by phenotypic and genetic correlations should be considered when selecting traits for the improvement in carcass merit. It is unlikely that all components of the USDA yield grade be necessarily evaluated in order to accurately rank sires with respect to carcass yield due to these dependencies; however, since YG is a composite trait, it may be of value in genetic evaluation. Sire genetic and phenotypic variances and covariances are reported for marbling score and Warner-Bratzler shear force in tables 3.16 and 3.17, respectively, and genetic parameters are summarized in table 3.18. Although the phenotypic correlation was negative and significantly different from zero, the genetic correlation between these traits was positive. This was contrary to the evidence reported by Van Vleck et al. (1994) and Koch et al. (1982) who reported a positive genetic correlation between MAR and WBS. The positive genetic correlation indicates that selection for increases in marbling score would have a correlated response of decrease in tenderness.

Table 3.16 Estimates of Sire Genetic, Residual and Phenotypic Variances (s.e.) for Meat Quality Traits.

Trait	Sire genetic variance	Residual variance	Phenotypic variance
MAR	0.8824 (.3209)	6.4704 (.3585)	7.3528 (.4614)
WBS	0.4251 (.2105)	6.6384 (.3674)	7.0634 (.4019)

Table 3.17 Estimates of Sire Genetic and Phenotypic Covariances (s.e.) for Meat Quality Traits[a].

Trait	MAR	WBS
MAR		-0.6579 (.3024)
WBS	.08327 (.1842)	

a Genetic covariance is on the lower diagonal, phenotypic covariance is on the upper diagonal.

able 3.18 Estimates of Heritabilities (h^2), Genetic (Rg) and Phenotypic (Rp) Correlations (s.e.) for Meat Quality Traits[a].

Trait	MAR	WBS
MAR	0.480 (.039)	-0.091 (.0417)
WBS	0.136 (.3005)	0.241 (.029)

a Heritabilities are on the diagonal, genetic correlation is on the lower diagonal, phenotypic correlation is on the upper diagonal.

Table 3.19 Estimates of Sire Genetic and Phenotypic Covariances (s.e.) Among Feedlot Performance, Carcass Composition and Meat Quality Traits.

	Sire genetic covariance			Phenotypic covariance		
Trait	WTONF	FDG	SWT	WTONF	FDG	SWT
HCW	31.277	0.4357	100.28	376.09	3.089	993.08
	(16.62)	(.1730)	(40.14)	(29.50)	(.2429)	(62.62)
FAT	0.4846	-0.0038	0.1785	2.738	0.0271	9.211
	(.5100)	(.0049)	(1.065)	(.888)	(.0070)	(1.656)
REA	3.934	0.0469	14.255	54.793	0.3383	124.36
	(3.713)	(.0369)	(8.366)	(6.810)	(.0528)	(13.02)
WAR	0.0867	0.0010	0.3139	1.207	0.0075	2.739
	(.0818)	(.0008)	(.1843)	(.1500)	(.0012)	(.2867)
KPH	-0.2679	0.0031	0.5720	1.976	0.0542	13.264
	(.5164)	(.0053)	(1.122)	(.8433)	(.0071)	(1.652)
MAR	-0.1735	0.0199	4.5523	3.898	0.1376	31.538
	(1.491)	(.0156)	(3.361)	(2.491)	(.0210)	(4.856)
WBS	-0.0831	-0.0044	-0.7225	-2.155	-0.0460	-10.91
	(1.200)	(.0121)	(2.583)	(2.354)	(.0183)	(4.305)

Sire genetic and phenotypic covariances among feedlot performance and carcass composition traits are given in table 3.19. The corresponding genetic and phenotypic correlations are given in table 3.20. Generally, weight and muscle characteristics had positive genetic correlations. This result was expected since it is assumed that increases in weight should be under the control of similar genes and those genes also have an effect on the size of muscles. The genetic correlations of hot carcass weight with feedlot performance traits were highest, ranging from 0.747 with weight on feed, 0.840 with feedlot daily gain to 0.972 with slaughter weight. Koch (1978) and Koch et al. (1982) also showed high positive genetic and phenotypic correlations between postweaning growth and HCW. The genetic correlation of slaughter weight with ribeye area and carcass weight adjusted ribeye area was 0.543, again indicating the strong genetic relationship between traits associated with growth rate and muscling. Lamb et al. (1990) and Wilson et al. (1993) found positive genetic and phenotypic correlations between postweaning gain and REA. Phenotypic correlations were positive between feedlot performance traits and all carcass composition traits and marbling score. The phenotypic correlations among feedlot performance traits and Warner-Bratzler shear force were negative, indicating a desirable phenotypic association between increased growth rate and weights and tenderness. Koch et al. (1982) found near zero phenotypic and genetic correlations between

Table 3.20 Estimates of Genetic (Rg) and Phenotypic Correlations (s.e.) Among Feedlot Performance, Carcass Composition and Meat Quality Traits.

	Genetic correlation (Rg)			Phenotypic correlation (Rp)		
Trait	WTONF	FDG	SWT	WTONF	FDG	SWT
HCW	0.747 (.163)	0.840 (.093)	0.972 (.024)	0.610 (.025)	0.694 (.022)	0.918 (.006)
FAT	0.310 (.295)	-0.198 (.255)	0.046 (.274)	0.128 (.040)	0.175 (.045)	0.245 (.041)
REA	0.369 (.286)	0.356 (.234)	0.543 (.206)	0.346 (.036)	0.295 (.040)	0.447 (.034)
WAR	0.369 (.286)	0.356 (.234)	0.543 (.206)	0.346 (.036)	0.295 (.040)	0.447 (.034)
KPH	-0.155 (.299)	0.145 (.233)	0.134 (.251)	0.099 (.042)	0.374 (.042)	0.376 (.039)
MAR	-0.035 (.303)	0.327 (.217)	0.375 (.227)	0.065 (.041)	0.318 (.042)	0.300 (.040)
WBS	-0.024 (.252)	-0.103 (.282)	-0.086 (.303)	-0.037 (.040)	-0.109 (.042)	-0.106 (.041)

postweaning gain and WBS; however, Shackelford et al. (1994) reported that the genetic correlation between postweaning growth and WBS was -0.44.

These results support the general trend in the literature regarding additive genetic effects on, and genetic parameters for, carcass traits. Heritability estimates for feedlot performance and carcass traits were moderate to large, and similar to the estimates reported in the literature. Standard errors were large for genetic correlations, and generally, only those with values greater than approximately 0.750 were significantly different from zero. The genetic correlation between MAR and WBS was positive (unfavorable), but close to zero, which agrees with the summary of Marshall (1994) who stated that genetic correlations of shear force with other carcass traits were either favorable or close to zero. Further study of the genetic relationships between preweaning growth and carcass traits and between reproductive traits and carcass traits is needed.

CHAPTER 4

HERITABILITIES AND ADDITIVE AND NON-ADDITIVE GENETIC EFFECTS FOR POSTWEANING GROWTH, CARCASS COMPOSITION AND MEAT QUALITY TRAITS AMONG BRAHMAN-INFLUENCED BEEF STEERS (PHASE II)

Introduction

Beef cattle genetic improvement programs have traditionally focused primarily on live animal growth traits. However, as consumers become more concerned with diet-health issues and as the beef industry focuses more on value-based marketing, emphasis on body composition traits is expected to become increasingly important in the design of breeding programs (Marshall, 1994). Traits associated with postweaning growth, under forage-based stocker programs and under high concentrate feed-based finishing programs, have not been extensively studied. Further, the variability in slaughter end point affects estimates of genetic parameters for traits associated with postweaning growth, carcass composition and meat quality.

Crossbreeding has become the predominant system of mating in the U.S. beef industry. By providing for the use of additive and non-additive genetic variation among and within breeds, crossbreeding, along with sound selection procedures can increase the efficiency of production in the beef enterprise.

The need for cattle adapted to the environment in which they produce is well documented. The sub-tropical climate of the Gulf Coast Region of the

United States has resulted in extensive use of *Bos indicus*, especially Brahman, genetics in crossbreeding programs. Brahman genetics are used in other regions of the U.S. as well. However, the price discrimination received for calves exhibiting heavy Brahman influence has prompted cattlemen and researchers to investigate alternative breeding programs designed to moderate the phenotypic expression of Brahman character in calves while maintaining environmental adaptability and heterosis levels in the herd (Crews, 1992). These programs include crossbreeding using Brahman-derivative breeds and the use of tropically adapted *Bos taurus* breeds.

The objectives of the present study were to estimate genetic parameters for eleven postweaning growth, carcass composition and meat quality traits in a multi-generation crossbreeding study involving the Angus, Brahman, Charolais and Hereford breeds; to estimate contrasts of direct and maternal additive breed effects for these traits; and to estimate the effects of direct and maternal heterosis on postweaning growth and carcass traits.

Materials and Methods

Data Collection and Cattle Management. Eleven postweaning growth performance, carcass composition and meat quality variables were recorded from steers (N = 1530) produced as part of a multi-generation crossbreeding study conducted between 1970 and 1988 at the LSU Crossbred Beef Cattle Research Unit, Baton Rouge. The environment is subtropical with average minimum and maximum daily temperatures of 13 and 26° C, average minimum

and maximum daily humidity of 54 and 88%, and an average annual rainfall of 147 cm. Purebred bulls representing the Angus, Brahman, Charolais and Hereford breeds were mated to produce straightbred, F_1, back-cross, three-breed cross, and 2-, 3- and 4-breed rotational crossbred calves. The crossbreeding design was constrained such that all non-purebred calves contained some percentage Brahman influence. A detailed comparison of generations and mating systems with respect to carcass traits was presented by DeRouen et al. (1992). The mating scheme resulted in non-overlapping generations. All calves were born between mid-January and mid-April of each year, and were weighed and identified at birth. Bull calves were castrated at an average age of 135 d and then weaned at an average age of 220 d, during the first week in October. Most steers born in this program were placed on a backgrounding program following weaning for 60 d, followed by a forage-based stocker program for approximately 150 d. Some steers were placed directly into the feedlot after weaning. During the stocker period, steers grazed annual ryegrass (*Lolium multiflorum)* prior to being placed in the feedlot. During the finishing phase, steers were fed a corn-based diet for a period ranging from 0 to 200 d. Some steers were slaughtered directly off ryegrass. Age at slaughter was calculated for each steer.

Postweaning growth traits of interest included daily gain on ryegrass (RDG), feedlot daily gain (FDG) and slaughter weight (SWT). Following normal slaughter and processing procedures, USDA yield and quality factors were

measured, including hot carcass weight (HCW), fat thickness over the longissimus (ribeye) muscle opposite the 12 - 13th rib interface (FAT) and area of the longissimus (REA) muscle. USDA yield grade (FYG), carcass-weight adjusted ribeye area (WAR) and estimated total lean yield (TLY) (USDA, 1989) were calculated. Meat quality traits included USDA marbling score (MAR) and Warner-Bratzler shear force (WBS). The procedure for obtaining WBS involved removing a 3.8 cm thick longissimus steak from the 12th rib, which, at d-7 postmortem, was deep-fat fried in vegetable oil for 12 min at 135°C to an approximate internal temperature of 71°C. Three 2.54 cm cores were removed from the steak and the force (kg) required to shear the core was measured using a Warner-Bratzler shear device.

Data Analyses. Data were analyzed using the Multiple Trait Derivative Free Maximum Likelihood (MTDFREML) programs of Boldman et al. (1995). Estimates of contrasts among fixed effects, variance components and estimated breeding values were obtained using MTDFREML. Estimates of heritabilities, genetic and phenotypic correlations were calculated using the usual formulae (Van Vleck, 1992).

Single trait analyses were conducted on the eleven response variables using a mixed (animal) model of the form

$$y = X\beta + ZU + e$$

where

y = the vector of observations,

X = the known incidence matrix relating fixed effects to observations,

Z = the known incidence matrix relating random effects to observations,

β = the vector of unknown fixed effects solutions,

U = the vector of unknown random effects solutions and

e = the vector of random residuals unique to each observation.

Henderson's mixed model equations (MME) simplify the calculation of the estimators of β and U, denoted b and u, for this model. In general, the MME are

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z+G^{-1} \end{bmatrix} \begin{bmatrix} b \\ u \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}$$

with the following results:

$$E \begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} X\beta \\ 0 \\ 0 \end{bmatrix}$$

and

$$var \begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} V & ZG & R \\ GZ' & G & 0 \\ R & 0 & R \end{bmatrix}$$

where V = var (y) = Z G Z' + R and G = var (u) = A ⊗ G_0 with G_0 being the variance-covariance matrix of additive genetic animal effects. The matrix A is

the numerator relationship matrix for animals. The inverse of matrix G, $G^{-1} = A^{-1} \otimes G_0^{-1}$, was computed according to the rules of Henderson and Quaas (1976). The residual (co)variance matrix, R, was assumed to be diagonal for single trait analyses: $R = I \sigma_e^2$. Henderson et al. (1959) showed the b from his MME are best linear unbiased estimators (BLUE) of the fixed effects as from generalized least-squares and Henderson (1963) showed the u are best linear unbiased predictors (BLUP) of the random effects.

The REML procedure maximizes the part of the multivariate normal likelihood associated with random effects essentially after adjusting for estimates of the fixed effects. Harville (1977) and Searle (1979) developed an equivalent form of the multivariate normal log likelihood, Λ, that is important to derivative-free restricted maximum likelihood (DFREML):

$$\Lambda = -0.5[constant + \log|R| + \log|G| + \log|C| + y'Py]$$

where C is the full rank coefficient matrix for the MME and y'Py is the generalized residual sum of squares. This form of the likelihood is completely general in R and G and the sample of records, y. Often, evaluating the log likelihood is less confusing if instead of maximizing Λ, -2Λ is minimized. For the derivative free method used by MTDFREML, convergence for (co)variance components estimation is reached when the global maximum of the log likelihood is found. The convergence criterion for these analyses was set at the point where V (-2Λ) was less than 1.00×10^{-6}. The convergence criterion

was met in all single trait models within 300 rounds of iteration. Multiple runs (cold restarts) of these analyses were conducted to ensure that the global maximum had been found rather than a local maximum according to Boldman et al. (1995).

Fixed genetic effects were modeled using regression coefficients corresponding to the direct and maternal additive breed composition associated with each observation. Likewise, the direct heterotic fractions corresponding to English x English (DEEH), English x Brahman (DEBH), English x Charolais (DECH) and Brahman x Charolais (DBCH) breed interactions for steers were fit. Total maternal heterosis (TMH) levels for each observation were calculated as the sum of all additive breed x breed interactions in dams. Coefficients for direct and maternal additive and heterotic effects used as regressions in this analysis were generated using CANAGE (Gould and Crews, 1996), a set of FORTRAN routines designed for this purpose. In summary, a total of four direct additive and four maternal additive coefficients were calculated, corresponding to the fractions of A, B, C, and H breeding in the individual and dam, respectively. Four direct and one maternal heterotic coefficients (direct and maternal) corresponded to the fraction of expected breed heterozygosity in the individual and dam, respectively. Age of dam (yr), julian birth date (d) and age at slaughter (d) were included as covariates. Year of birth was also included as a fixed effect. To maintain full rank in the MME, the coefficients corresponding to direct and maternal additive Brahman effects were

constrained to a solution of zero. Additive and maternal direct breed contrasts of interest included all pairwise contrasts, and the contrast of Brahman versus the average non-Brahman additive and maternal genetic effects. Solutions for the four direct heterosis and the total maternal heterosis coefficients were also obtained. There were a total of 2584 animals in the inverse of the additive relationship matrix. Based on available information, no animals in these analyses were inbred. A maximum of N = 1530 steers had valid records for each of the 11 postweaning growth, carcass composition and meat quality traits. There were 142 sires represented in the data, with approximately 25% of the steers in each sire breed group. Bulls sired an average of 10.8 steer progeny. There were a total of 920 dams in the data, with each dam producing an average of 1.7 steer progeny (range = 1 to 4 steers).

Results and Discussion

Summary statistics for model covariates are summarized in table 4.1, and summary statistics for response variables are given in table 4.2. The fixed effects of interest included direct and maternal additive genetic effect contrasts and estimates of direct and maternal heterosis effects on postweaning growth, carcass composition and meat quality traits.

Direct Additive Genetic Effects. Direct additive genetic effect contrasts (table 4.3) were obtained for all possible pairwise breed comparisons. Daily gain on ryegrass during the stocker period (RDG) was not different ($P > .05$)

Table 4.1 Sample Summary Statistics for Model Covariates.

Covariate	N	MIN	MAX	AVG	STD
A, %	1530	0.0	100	23.68	32.34
B, %	1530	0.0	100	30.65	27.98
C, %	1530	0.0	100	21.39	31.84
H, %	1530	0.0	100	24.27	32.28
A(M), %	1530	0.0	100	24.03	33.38
B(M), %	1530	0.0	100	31.75	28.27
C(M), %	1530	0.0	100	19.64	32.35
H(M), %	1530	0.0	100	24.54	32.65
DEEH, %	1530	0.0	50.0	5.92	15.69
DEBH, %	1530	0.0	100	27.05	30.62
DECH, %	1530	0.0	75.0	8.47	19.24
DBCH, %	1530	0.00	100	12.95	23.80
TMH, %	1530	0.00	100	56.27	43.01
DAGE, yr	1530	2	19	5.78	2.33
JBD, d	1530	10	113	49.25	19.02
SAGE, d	1530	365	605	497	53.95

Table 4.2 Sample Summary Statistics for Response Variables.

Trait	N	MIN	MAX	AVG	STD
RDG, kg/d	1529	0.05	1.75	0.83	0.25
FDG, kg/d	1476	0.07	2.35	1.16	0.30
SWT, kg	1529	209	674	457	65.5
HCW, kg	1530	117	424	272	42.5
FAT, cm	1529	0.05	3.10	0.84	0.46
REA, cm^2	1530	45	130	71	11.7
WAR, cm^2	1530	18	44	26	3.8
FYG	1530	1.00	6.10	2.55	0.83
TLY, kg	1530	62	216	139	21.5
MAR	1530	1.00	8.30	4.02	0.96
WBS, kg	863	4.81	23.18	10.01	2.7

Table 4.3 Estimates of Direct Additive Genetic Effect Contrasts (s.e.) for Postweaning Growth Traits.

Contrast	RDG	FDG	SWT
A - B	0.172*	-0.007	-2.16
	(.04)	(.06)	(10.8)
A - C	-0.039	-0.134*	-65.98*
	(.04)	(.06)	(10.8)
A - H	-0.038	-0.059	-13.36
	(.04)	(.05)	(9.9)
B - C	-0.211*	-0.127*	-63.82*
	(.04)	(.06)	(11.2)
B - H	-0.210*	-0.052	-11.20
	(.05)	(.06)	(11.3)
C - H	0.001	0.075	52.62*
	(.04)	(.06)	(11.2)
B (DIR)	-0.197*	-0.057	-24.28*
	(.04)	(.05)	(9.3)

* $P < .05$.

among the direct additive effects of the Angus, Charolais and Hereford breeds. However, the direct additive effect of Brahman was from 0.172 to 0.211 kg per d lower than the effects of Angus, Hereford or Charolais. The direct additive Brahman effect on RDG was 0.197 kg per d smaller ($P < .05$) than the non-Brahman effect.

The direct additive breed contrasts for daily gain in the feedlot (FDG) showed that the effect of Charolais was larger ($P < .05$) than that of Angus and Brahman, but similar to Hereford. Direct additive breed contrasts involving the Brahman, Angus and Hereford were not significant. Although the effect of Charolais was 0.127 kg per d larger than that of Brahman, the contrast of Brahman versus non-Brahman genetic effects was near zero. However, the direct additive Brahman effect tended to be smaller than the average non-Brahman direct additive effect.

Weight at slaughter (SWT) was also similar among the Brahman, Angus and Hereford genetic effects. The direct additive effect of Charolais was larger than all other direct additive breed effects, being 65.98 kg larger than the Angus, 63.82 kg larger than the Brahman and 52.62 kg larger than the Hereford effects for SWT. The direct additive effect of Brahman was 24.28 kg smaller ($P <.05$) for SWT than the average non-Brahman effect. This probably resulted from the smaller direct additive Brahman effects on RDG and FDG relative to the non-Brahman effects.

Direct additive genetic effect contrasts for carcass composition traits are presented in table 4.4. Similar to SWT, hot carcass weights (HCW) were heaviest due to the Charolais effect. The direct additive effect of Charolais was from 39.88 to 42.14 kg larger for HCW than for Angus, Brahman or Hereford. Contrasts of direct additive genetic effects involving the Angus, Brahman and Hereford were not significant. However, the contrast of direct additive Brahman versus non-Brahman effects showed that the Brahman effect decreased HCW 15.26 kg relative to the average of non-Brahman effects. The Brahman versus non-Brahman direct additive contrast for HCW was only slightly larger than one-half of the corresponding contrast for SWT, which possibly indicated that the Brahman effect, although smaller for SWT, may be larger for dressing percentage compared to the non-Brahman effect.

Direct additive genetic effect contrasts for fat thickness opposite the ribeye at the 12^{th}-13^{th} rib (FAT) clearly showed that the Brahman effect decreased FAT compared to the Angus and Hereford effects. The direct additive effect of Brahman was 0.486 cm smaller than that of Angus and 0.433 cm smaller than that of Hereford, but 0.241 cm larger than that of Charolais. The contrast of Angus versus Hereford effects was not significant, and the direct additive effect of Charolais was smaller than both the Angus and Hereford. Therefore, the overall ranking of breeds based on direct additive breed effects reflected that the Charolais effect was leanest, with Brahman intermediate, and Angus and Hereford effects fattest but similar. Although the

Table 4.4 Estimates of Direct Additive Genetic Effect Contrasts (s.e.) for Carcass Composition Traits.

Contrast	HCW	FAT	REA	WAR
A - B	1.41	0.486*	0.55	-0.001
	(7.4)	(.09)	(2.5)	(.89)
A - C	-40.73*	0.728*	-18.42*	-2.336*
	(7.4)	(.09)	(2.5)	(.89)
A - H	-0.86	0.054	0.75	0.374
	(6.9)	(.08)	(2.4)	(.84)
B - C	-42.14*	0.241*	-18.97*	-2.34*
	(7.7)	(.09)	(2.6)	(.93)
B - H	-2.26	-0.433*	0.20	0.376
	(7.8)	(.09)	(2.6)	(.93)
C - H	39.88*	-0.674*	19.17*	2.71*
	(7.7)	(.09)	(2.6)	(.93)
B (DIR)	-15.26*	-0.226*	-6.44*	-0.653
	(6.4)	(.08)	(2.1)	(.76)

* $P < .05$.

direct additive effect of Brahman on FAT was larger than that of Charolais, the contrast of direct additive Brahman versus non-Brahman effects indicated that the Brahman effect was 0.226 cm less for FAT than the non-Brahman effect.

Individual direct additive genetic effect contrasts among the Brahman, Angus and Hereford for ribeye area (REA) were not significant. However, the direct additive effect of Charolais for REA was from 18.42 to 19.17 cm^2 larger than those of Brahman, Angus and Hereford. The direct additive effect of Brahman decreased ($P < .05$) REA by 6.44 cm^2 relative to the non-Brahman effect.

Carcass weight adjusted ribeye area (WAR) has been suggested as a better indicator of total carcass muscling because it accounts for differences in carcass weight (Crews, 1995). Larger carcasses are expected to have more REA, but that increase in muscle size may not be proportional to the increase in HCW, therefore, WAR is becoming a more widely referenced measure of muscling in studies of carcass composition. The direct additive breed effects contrasts for WAR indicated that the effects of the Angus, Brahman and Hereford breeds were similar. However, the direct additive effect of Charolais was from 2.34 to 2.71 cm^2 larger than for Angus, Brahman and Hereford. The contrast of direct additive Brahman versus non-Brahman genetic effects was also not significant, indicating that although the Brahman effect decreased REA, when HCW was accounted for, the differences in Brahman versus non-Brahman genetic effects were diminished. It may be concluded therefore, that

the negative genetic effect of Brahman on REA was proportional to the negative genetic effect on HCW relative to the non-Brahman effects.

Direct additive genetic effect contrasts for carcass yield and meat quality traits are given in table 4.5. Final USDA yield grade (FYG) was similar between Angus and Hereford. The contrasts between Angus and Brahman and between Angus and Charolais effects indicated that the direct additive effect of Angus increased yield grade, or decreased percentage of carcass weight expected to be derived as boneless, closely trimmed retail beef. The direct additive effect of Hereford on FYG was also larger than that of Brahman and Charolais. The direct additive effect of Charolais on FYG was smaller than that of Brahman. Therefore, similar to the results observed for FAT, ranking of genetic effects for FYG indicated that the Charolais effect increased FYG least, with Brahman intermediate, and Angus and Hereford similar. FYG is calculated using a regression equation involving HCW, FAT, REA and the percentage of carcass weight as fat in the kidney, pelvic and heart (KPH) regions (USDA, 1989). Crews (1995; 1996) has reviewed research indicating that FAT tends to influence FYG among carcasses with similar HCW more than other factors in the equation, which is supported by the present results indicating that differences in FYG were highly similar to differences in FAT.

Estimated percent carcass lean yield can be predicted using HCW, FAT, REA and KPH in a similar regression equation to that of FYG (USDA, 1989). Multiplication of percent lean yield by HCW results in total carcass lean yield

Table 4.5 Estimates of Direct Additive Genetic Effect Contrasts (s.e.) for Carcass Yield and Meat Quality Traits.

Contrast	FYG	TLY	MAR	WBS
A - B	0.569*	0.79	1.48*	-4.21*
	(.16)	(3.9)	(.19)	(1.5)
A - C	1.29*	-28.57*	0.90*	-0.90
	(.16)	(3.9)	(.19)	(.72)
A - H	-0.026	-2.27	0.48*	-0.13
	(.15)	(3.7)	(.17)	(.59)
B - C	0.721*	-29.36*	-0.58*	3.31*
	(.17)	(4.0)	(.19)	(1.5)
B - H	-0.594*	-3.06	-1.00*	4.08*
	(.17)	(4.0)	(.20)	(1.6)
C - H	-1.32*	26.30*	-0.43*	0.77
	(.17)	(4.0)	(.18)	(.76)
B (DIR)	-0.147	-11.07*	-1.03*	3.86*
	(.14)	(3.3)	(.16)	(1.5)

* $P < .05$.

(TLY) expected from the beef carcass. An implication of this calculation is that heavier carcasses would be expected to have higher TLY than lighter carcasses with similar FYG. Direct additive breed contrasts for TLY are also given in table 4.5. The direct additive effect of Charolais increased ($P < .05$) TLY by 28.57 kg versus Angus, by 29.36 kg versus Brahman and by 26.30 kg versus Hereford. The direct additive advantage in leanness of Charolais combined with the direct additive effect of Charolais to increase carcass weight makes these results expected. Effects on TLY among Brahman, Angus and Hereford tended to be similar; however, the contrast of direct additive Brahman versus non-Brahman effects was significantly negative, indicating that the genetic effect of Brahman decreased TLY 11.07 kg relative to the non-Brahman effect.

All direct additive breed contrasts obtained with regard to marbling score (MAR) were significant. The overall breed ranking based on direct additive effect contrasts placed the Brahman effect most negative for marbling scores. The direct additive effect of Charolais on MAR was positive, whereas the Brahman effect was negative, but was less positive than the Hereford effect. The direct additive effect of Angus on MAR was largest; 1.48 units larger than that of Brahman, 0.90 units larger than that of Charolais and 0.48 units larger than that of Hereford. The direct additive contrast of Brahman versus non-Brahman effects indicated that the Brahman effect significantly lowered MAR relative to the average non-Brahman effect.

The direct additive effect contrasts for tenderness as measured by Warner-Bratzler shear (WBS) force among Angus, Hereford and Charolais were not significant. However, the direct additive breed effect of Brahman was from 3.31 to 4.21 kg larger than those of the Angus, Charolais and Hereford. Likewise, the direct additive contrast of Brahman versus non-Brahman indicated that the Brahman effect increased WBS values 3.86 kg versus the non-Brahman effect. This represents a highly significant decrease in tenderness due to Brahman influence.

Maternal Additive Genetic Effects. Maternal additive breed effects were discussed for carcass traits by DeRouen et al. (1992). Based on the additive breed composition of the dam, maternal additive breed effects are interpreted as genetic influences expressed in the dam that affect progeny phenotype, independent of the genes she transmits directly to her progeny. Since the additive breed composition of the steer was accounted for by the direct additive breed coefficients discussed earlier, the following contrasts involving maternal additive breed effects will be presented.

Maternal additive genetic effects on postweaning growth traits are presented in table 4.6. The only maternal additive breed effect contrast that was signficant for RDG was that between the Charolais and Hereford. The maternal additive effect of Charolais increased RDG 0.088 kg per d versus the Hereford. The maternal additive contrast of Brahman versus non-Brahman was not significant.

Table 4.6 Estimates of Maternal Additive Genetic Effect Contrasts (s.e.) for Postweaning Growth Traits.

Contrast	RDG	FDG	SWT
A - B	0.009 (.04)	0.210* (.05)	20.16* (8.9)
A - C	-0.066 (.04)	0.009 (.05)	-17.53* (8.4)
A - H	0.022 (.04)	0.068 (.04)	16.11* (8.0)
B - C	-0.057 (.04)	-0.200* (.05)	-37.68* (9.1)
B - H	0.031 (.04)	-0.146* (.05)	-4.045 (9.5)
C - H	0.088* (.04)	0.054 (.05)	33.64* (9.1)
B (MAT)	-0.006 (.03)	-0.186* (.04)	-20.63* (7.3)

* $P < .05$.

Maternal additive breed effects contrasts with regard to FDG involving the Brahman were significant. The maternal additive effect of Brahman on FDG was from 0.146 to 0.210 kg per d lower than those of the Angus, Charolais and Hereford. Similarly, the maternal additive effect of Brahman on FDG was 0.186 kg per d smaller than that of non-Brahman.

Maternal additive effects on SWT are also presented in table 4.6. The maternal additive effect of Angus on SWT was 20.16 kg larger than that of Brahman, 16.11 kg larger than that of Hereford, but 17.53 kg smaller than that of Charolais. The maternal additive effect of Charolais on SWT was 37.68 kg larger than that of Brahman and 33.64 kg larger than that of Hereford. The maternal additive effects of Brahman and Hereford on SWT were not significantly different. The contrast of maternal additive Brahman versus non-Brahman was 20.63 kg in favor of the non-Brahman. It is likely that maternal additive effects at weaning carried over to slaughter weight since maternal additive effects on RDG and FDG were generally smaller than on SWT.

Maternal additive effects on carcass composition traits are presented in table 4.7. Maternal additive effects contrasts among the Brahman, Angus and Hereford breeds were not significant. However, the maternal additive effect of Charolais on HCW were significant, from 14.16 to 26.06 kg larger than those of the Angus, Hereford and Brahman. The maternal additive effect of Brahman was 14.32 kg smaller for HCW than that of non-Brahman. These

Table 4.7 Estimates of Maternal Additive Genetic Effect Contrasts (s.e.) for Carcass Composition Traits.

Contrast	HCW	FAT	REA	WAR
A - B	11.90	0.035	3.46	0.074
	(6.1)	(.07)	(1.96)	(.711)
A - C	-14.16*	-0.171*	0.467	1.404*
	(5.8)	(.07)	(.187)	(.676)
A - H	6.89	-0.034	1.021	-0.344
	(5.5)	(.07)	(1.79)	(.648)
B - C	-26.06*	-0.206*	-2.989	1.330
	(6.3)	(.08)	(2.01)	(.729)
B - H	-5.01	-0.002	-2.435	-0.418
	(6.6)	(.08)	(2.10)	(.763)
C - H	21.05*	0.205*	0.554	-1.748*
	(6.2)	(.08)	(1.99)	(.725)
B (MAT)	-14.32*	-0.081	-2.959	0.279
	(5.3)	(.06)	(1.71)	(.620)

* $P < .05$.

results indicate that maternal additive effects tended to decrease from postweaning traits to carcass traits, although the maternal additive effects of Charolais remained significantly positive.

Similar to HCW, maternal additive effects on FAT were not significant with the exception of those contrasts involving the Charolais. The maternal additive effect of Charolais was 0.171 cm larger than that of Angus, 0.206 cm larger than that of Brahman and 0.205 cm larger than that of Hereford. The contrast of maternal additive Brahman versus non-Brahman was not significantly different from zero. All maternal additive effects contrasts for REA were small and near zero. Similar to REA, maternal additive effects on WAR tended to be small. The maternal additive effect of Charolais on WAR was 1.40 cm^2 smaller than that of Angus and 1.75 cm^2 smaller than that of Hereford but only tended to be smaller than that of Brahman.

Maternal additive effect contrasts for carcass yield and meat quality traits are given in table 4.8. Final USDA yield grade (FYG) was not significantly affected by maternal additive effects among the Angus, Hereford and Brahman breeds. However, similar to the trends observed for HCW, FAT and WAR, the maternal additive effect of Charolais was 0.299 FYG units larger than that of Angus, 0.327 units larger than that of Brahman and 0.429 units larger than that of Hereford. The contrast of maternal additive Brahman versus non-Brahman was near zero (0.086 FYG units). Estimated total lean yield (TLY) showed a very similar pattern to FYG with regard to maternal

Table 4.8 Estimates of Maternal Additive Genetic Effect Contrasts (s.e.) for Carcass Yield and Meat Quality Traits.

Contrast	FYG	TLY	MAR	WBS
A - B	0.033	3.22	0.032	0.53
	(.133)	(3.07)	(.156)	(1.48)
A - C	-0.299*	-6.29*	-0.095	0.96
	(.126)	(2.92)	(.149)	(.589)
A - H	0.135	4.54	0.066	-0.41
	(.121)	(2.80)	(.142)	(.521)
B - C	-0.327*	-9.51*	-0.063	0.43
	(.136)	(3.15)	(.160)	(1.39)
B - H	0.102	1.31	-0.098	-0.94
	(.143)	(3.29)	(.169)	(1.59)
C - H	0.429*	10.82*	0.161	-1.26
	(.136)	(3.13)	(.161)	(.652)
B (MAT)	-0.086	-3.81	0.023	-0.34
	(.116)	(2.68)	(.136)	(1.45)

* $P < .05$.

additive effects. These results indicated that the maternal additive effect of Charolais increased TLY compared to those of the Angus, Brahman and Hereford. Since the maternal additive effect of Charolais was positive relative to the other breeds for FYG, the positive maternal additive effects of Charolais for TLY can be most likely attributed to the positive maternal additive effects of Charolais on HCW rather than for FYG. Since higher FYG designate lower yielding carcasses, the combination of positive maternal additive effects of Charolais on FYG and TLY must include a highly positive maternal additive effect of Charolais on HCW.

Maternal additive effects on USDA marbling score (MAR) and tenderness as measured by Warner-Bratzler shear (WBS) force were not significant. In fact, all maternal additive effects contrasts for MAR were very close to zero.

Direct and Total Maternal Heterosis. Estimates of the four direct heterosis and the total maternal heterosis coefficients for postweaning growth traits are presented in table 4.9. Contrasts of direct heterosis coefficients were not obtained. All direct heterosis effects were significant for RDG. The direct Brahman x English (Angus or Hereford) heterotic effect was largest, with a value of 0.324 kg per d on RDG. The English x English (Angus x Hereford and Hereford x Angus) and English (Angus or Hereford) x Charolais heterotic effects were similar (0.190 and 0.193 kg/d, respectively). The Brahman x Charolais heterotic effect was intermediate, with a positive value of 0.309 kg

Table 4.9. Estimates of Direct and Maternal Heterosis Effects (s.e.) for Postweaning Growth Traits.

Effect	RDG	FDG	SWT
DEEH	0.189*	0.113	45.97*
	(.044)	(.057)	(9.94)
DEBH	0.324*	0.117*	71.49*
	(.036)	(.048)	(8.21)
DECH	0.193*	0.084	33.48*
	(.045)	(.058)	(10.08)
DBCH	0.309*	0.089	51.14*
	(.040)	(.053)	(8.99)
TMH	-0.194*	0.008	5.09
	(.029)	(.039)	(6.67)

* $P < .05$.

per d on RDG. Direct heterosis effects were generally not significant for FDG, with the exception of the English x Brahman effect, which increased FDG by 0.117 kg per d. All direct heterosis effects were significant ($P < .05$) for SWT. The largest increase was due to English x Brahman heterosis, followed by the Brahman x Charolais, English x English and English x Charolais effects. The estimate obtained for total maternal heterosis effects on RDG was negative, with a value of -0.194 kg per d.

Estimates of the effects of direct and maternal heterosis on carcass composition traits are given in table 4.10. All direct heterosis effects on HCW were significant and positive, ranging from 23.31 kg for the English (Angus or Hereford) x Charolais coefficient to 49.52 kg for the English x Brahman coefficient. The English x English and Brahman x Charolais heterotic effects on HCW were intermediate and similar. Although the total maternal heterosis effects on HCW were positive (1.46 kg), this estimate was not sigificantly different from zero.

With respect to FAT and REA, the only heterotic effect found to be significant was the English x Brahman (DEBH). The DEBH coefficient had a 0.183 cm positive effect on FAT and a 4.29 cm^2 positive effect on REA. Total maternal heterosis effects on both REA and FAT were near zero. Carcass weight adjusted ribeye area was significantly and negatively affected by all four direct heterosis effects. The largest negative effect was observed for

Table 4.10 Estimates of Direct and Maternal Heterosis Effects (s.e.) for Carcass Composition Traits.

Effect	HCW	FAT	REA	WAR
DEEH	33.99*	0.079	3.75	-1.90*
	(6.84)	(.084)	(2.13)	(.078)
DEBH	49.52*	0.183*	4.29*	-3.24*
	(5.64)	(.069)	(1.74)	(.642)
DECH	23.31*	0.073	-1.85	-2.75*
	(6.93)	(.085)	(2.15)	(.789)
DBCH	34.77*	0.130	1.75	-2.56*
	(6.18)	(.076)	(1.90)	(.701)
TMH	1.46	0.041	2.74	0.711
	(4.59)	(.056)	(1.43)	(.525)

* $P < .05$.

DEBH (-3.24 cm^2). The total maternal heterotic effect on WAR tended to be positive, but was not significant (0.711 cm^2).

Direct heterosis effects on FYG, TLY and MAR were positive (table 4.11). Direct heterosis increased TLY from 14.07 kg to 30.43 kg. However, total maternal heterotic effects on FYG, TLY and MAR were negative, with the total maternal heterotic effect on TLY significantly negative (-4.74 kg). Direct and total maternal heterosis effects on WBS were not significant.

Genetic Parameters. Estimates of additive genetic, residual and phenotypic variances for postweaning growth traits are given in table 4.12, and heritabilities are presented in table 4.13. The heritability of RDG (0.065) was near zero, but the heritabilities of FDG and SWT (0.183 and 0.321, respectively) were moderate. The estimated heritability of FDG was lower than that of Reynolds et al. (1991) who reported that gain on feeding test heritability was 0.50 using a sire-son regression model. However, the estimate of 12- to 20-month gain heritability given by DeNise and Torabi (1989) was lower (h^2 = 0.24). Likewise Reynolds et al. (1991) reported a heritability estiamte of 0.49 for slaughter weight among Herefords. Also, DeNise and Torabi (1989) reported that the heritability of 20-month weight was 1.00 in bulls and 0.44 in heifers.

Estimates of additive genetic, residual and phenotypic variances (table 4.14) for carcass composition and meat quality traits indicated that these traits had moderate to high heritabilites (tables 4.15 and 4.16). Carcass

Table 4.11 Estimates of Direct and Maternal Heterosis Effects (s.e.) for Carcass Yield and Meat Quality Traits.

Effect	FYG	TLY	MAR	WBS
DEEH	0.184	18.76*	0.204	0.660
	(.148)	(3.36)	(.179)	(.606)
DEBH	0.428*	30.43*	0.211	-2.232
	(.122)	(2.76)	(.148)	(1.21)
DECH	0.298	14.07*	0.194	-0.588
	(.150)	(3.39)	(.182)	(.735)
DBCH	0.409*	22.69*	0.235	-2.209
	(.134)	(3.02)	(.162)	(1.18)
TMH	-0.052	-4.74*	-0.181	0.433
	(.099)	(2.26)	(.120)	(.887)

* $P < .05$

Table 4.12 Estimates of Additive Genetic, Residual and Phenotypic Variances for Postweaning Growth Traits.

	Additive genetic	Residual	Phenotypic
RDG	0.00242	0.03452	0.03695
FDG	0.01050	0.04703	0.05754
SWT	569.894	1205.160	1775.054

Table 4.13 Estimates of Heritabilities (h^2) for Postweaning Growth Traits.

h^2	RDG	FDG	SWT
RDG	0.065		
FDG		0.183	
SWT			0.321

Table 4.14 Estimates of Additive Genetic, Residual and Phenotypic Variances for Carcass Composition and Meat Quality Traits.

	Additive genetic	Residual	Phenotypic
HCW	273.119	566.047	839.166
FAT	0.0318	0.0951	0.1269
REA	42.516	36.929	79.445
WAR	4.8398	5.9436	10.783
FYG	0.1412	0.2506	0.3918
TLY	94.580	104.834	199.414
MAR	0.1319	0.4509	0.5828
WBS	0.8353	4.5300	5.3653

Table 4.15 Estimates of Heritabilities (h^2) for Carcass Composition Traits.

h^2	HCW	FAT	REA	WAR
HCW	0.325			
FAT		0.251		
REA			0.535	
WAR				0.449

Table 4.16 Estimates of Heritabilities (h^2) for Carcass Yield and Meat Quality Traits.

h^2	FYG	TLY	MAR	WBS
FYG	0.360			
TLY		0.474		
MAR			0.226	
WBS				0.156

composition traits ranged in heritability from 0.251 for FAT to 0.535 for REA. The heritability estimate for HCW (h^2 = 0.325), was similar to the estimates of Lamb et al. (1990), Reynolds et al. (1991), Veseth et al. (1993) and Wilson et al. (1993) who reported heritabilities for HCW in the range of 0.31 to 0.38. The estimates of Koch (1978), Koch et al. (1982), Benyshek (1981) and MacNeil et al. (1984) were generally larger, ranging from 0.41 to 0.68. Gregory et al. (1995) estimated the heritability of HCW to be 0.23 among purebred and composite steers produced at the Meat Animal Research Center. The heritability of FAT in these data was estimated to be 0.251. Lamb et al. (1990) found the heritability of fat thickness to be 0.24 in a study involving Herefords, and Wilson et al. (1993) reported a heritability of 0.26 for FAT based on Angus field records. Other researchers have reported that the heritability of FAT was higher than in the present study (Koch, 1978; Koch et al., 1982; Benyshek, 1981; MacNeil et al., 1991). Marshall (1994) summarized the results of six genetic studies and reported an average heritability of 0.44 for FAT. The heritability of REA (h^2 = 0.535) was the highest among carcass traits studied. Most reports of heritability for longissimus muscle area in the literature have been high (Koch et al., 1982; Benyshek, 1981; Arnold et al., 1991; Van Vleck et al., 1992; Veseth et al., 1993). However, the estimates of heritability for REA were lower in some studies compared to the present study (Koch, 1978; Lamb et al., 1990; Wilson et al., 1993; Gregory et al., 1995). The heritability of carcass-weight

adjusted ribeye area (0.449) was, as expected, intermediate to that of hot carcass weight and ribeye area. Estimates of heritability for this trait have been unavailable. The heritability estimates for FYG (0.360), TLY (0.474) and MAR (0.226) were higher than that for Warner-Bratzler shear force (0.156). Several researchers have reported heritabilities for traits similar to FYG and TLY. Shackelford et al. (1994) reported the heritability of actual retail product weight to be 0.47 which was similar to the estimate found here for TLY. Similarly, percent retail cuts (which can be used to calculate TLY with HCW) has been studied. Koch et al. (1982) reported that actual percent retail cuts had a heritability of 0.63. Benyshek (1981) reported a heritability of 0.49 for percent retail cuts. Other researchers have reported lower estimates for the heritability of this trait (Lamb et al., 1990; Woodward et al., 1992). Marshall (1994) reported, based on five studies, an average heritability for percent retail cuts of 0.26. Generally, heritability estimates in the literature for marbling score have been moderate to high, ranging from 0.23 to 0.47. Estimates in the literature of the heritability of WBS have been highly variable, ranging from 0.09 (Van Vleck et al., 1992) to 0.71 (Shackelford et al., 1994). The estimates of Koch et al. (1982) and Gregory et al. (1995) were intermediate. Therefore, the present results generally agree with previous studies which have found that carcass traits are moderately to highly heritable. The possible exception to this was Warner-Bratzler shear force, however, few estimates of heritability have been reported for this trait and the estimates in the literature

have been highly variable. The moderate to high heritability estimates obtained for carcass composition traits clearly indicate that genetic change could be accomplished through selection. However, the genetic and phenotypic relationships of carcass traits with early life measures and with reproductive traits must be established before recommendations for selection can be made. Since the heritabilities of TLY, WAR and FYG tended to be moderately high to high, it may be optimal to concentrate on these traits rather than the component traits used to derive them.

Since selection response is slowed by increasing the number of traits under selection, reducing the number of carcass traits to a minimum might be more optimal. Scientists have recently provided genetic analyses of traits referred to as those associated with total "carcass merit" which generally summarize two general characteristics: lean yield and meat quality. The potential drawback of composite traits such as FYG and TLY is that they tend to have more variable heritability estimates as reported in the literature and those estimates depend on the genetic variability of the underlying single traits. Also, as molecular genetic research continues to search for quantitative trait loci controlling carcass merit, the probability of these composite measures of carcass merit being under the control of a single or few genes will be expected to be less than the probability that individual carcass composition measures are under the control of major genes. This makes it less likely that rapid selection of composite traits to improve carcass merit with the use of the

major gene approach would be effective. One alternative that has not been addressed sufficiently in the literature is the combined approach of not only increasing the use of germ plasm resources which tend to increase carcass merit, but also decrease the use of those resources which tend not to produce acceptable carcasses in the current industry. In general, selection for carcass composition has been largely ignored in the literature and in the beef industry. The expense and time involved is a limitation of long-term selection studies in beef cattle.

CHAPTER 5

GENETIC AND PHENOTYPIC CORRELATIONS FOR POSTWEANING GROWTH, CARCASS COMPOSITION AND MEAT QUALITY TRAITS (PHASE II)

Introduction

Crossbreeding has become the predominant system of mating in the U.S. beef cattle industry. Crossbreeding allows for the efficient use of additive and non-additive genetic variation among breeds which, with accurate selection procedures, can improve the productivity of the beef enterprise. Numerous researchers have reviewed experimental results which establish the efficacy of planned crossbreeding systems (Franke, 1980, Cundiff, 1980, Turner, 1980). The selection of breeds to be used in a crossbreeding system and the traits which are selected should have economic value.

The recent development of mixed model methods and increases in computing power have enabled scientists to estimate breeding values for animals as potential parents. Traits associated with economic value in the beef industry are numerous, and often, these traits have antagonistic genetic relationships. In order to optimize response to selection for economically important traits, the beef producer must be aware of the genetic and phenotypic relationships among traits under selection. The estimation of these genetic parameters (genetic and phenotypic correlations) has become more efficient with the development of the animal model and software written to implement the animal model and related mixed models.

The importance of traits associated with postweaning growth, feedlot performance, carcass composition and meat quality have recently received greater attention in the scientific literature. As consumers continue to demand lean and consistently palatable beef, consideration of these traits in the design of selection programs will become increasingly important. Further, as the beef industry continues to move toward a value-based marketing system, the importance of end-product traits will increase.

A large portion of the cow-calf segment of the beef industry is located in the Gulf Coast Region of the United States, where environmental demands have prompted the widespread use of tropically adapted breeds including *Bos indicus* breeds such as the Brahman. Use of Brahman inheritance in crossbreeding programs results in the production of calves with distinct *Bos indicus* characteristics which are often discriminated against by the feeder and packer segments of the beef industry. This discrimination can be attributed to less desirable carcass composition and meat quality often found among cattle with heavy Brahman influence. However, few reports are available in the literature which evaluate crossbreeding designs including the Brahman with the objective of estimating genetic correlations among postweaning growth, feedlot performance, carcass composition and meat quality traits. These estimates will be necessary in the development of crossbreeding programs and selection strategies for the optimal production of beef. Also, genetic relationships among traits of economic importance should be evaluated.

The objective of the present study was to estimate phenotypic and genetic correlations among traits associated with postweaning growth, feedlot performance, carcass composition and meat quality using data from a multi-generation crossbreeding study involving the Angus, Brahman, Charolais and Hereford breeds.

Materials and Methods

Data Collection and Cattle Management. Data were available from steers (N = 1530) produced in a multi-generation crossbreeding study involving the Angus, Brahman, Charolais and Hereford breeds. Steers were produced from 1970 to 1988 at the Louisiana State University Agricultural Center Ben Hur Crossbred Beef Cattle Research Unit in Baton Rouge. The environment is subtropical with average minimum and maximum daily temperatures of 13 and 26°C, average minimum and maximum daily humidity of 54 and 88%, and an average annual rainfall of 147 cm. Calves were born during spring calving seasons and bull calves were castrated at an average age of 135 d and then weaned at an average age of 220 d during the first week in October. Following weaning, steers were placed on a backgrounding program for 60 d, followed by a forage-based stocker program for approximately 150 d. During the stocker period, steers grazed annual ryegrass (*Lolium multiflorum*) prior to being placed in the feedlot. During the feedlot phase, steers were fed a corn based high energy diet for a period ranging from 0 to 200 d. Age at slaughter was calculated for each steer.

Purebred bulls representing the Angus, Brahman, Charolais and Hereford breeds were mated to purebred and crossbred cows to produce straightbred, F_1, back-cross, three-breed cross, and 2-, 3- and 4-breed rotational crossbred calves. A detailed comparison of generations and mating systems with respect to postweaning growth and carcass traits was given by DeRouen et al. (1992). The mating system was designed such that generations were non-overlapping and all crossbred calves contain some percentage Brahman.

Postweaning growth traits of interest included daily gain on ryegrass (RDG), feedlot daily gain (FDG) and slaughter weight (SWT). Following normal slaughter procedures, carcass composition traits were measured, including hot carcass weight (HCW), fat thickness over the longissimus muscle at the 12-13th rib interface (FAT), and area of the exposed face of the longissimus muscle at the 12-13th rib interface (REA). USDA yield grade (FYG), total lean yield (TLY) and carcass weight adjusted ribeye area (WAR) were calculated (USDA, 1989). Meat quality traits of interest included USDA marbling score (MAR) and Warner-Bratzler shear force (WBS). The procedure for obtaining WBS involved removing a 3.8 cm thick longissimus steak from the 12th rib region of the carcass, which, at d-7 postmortem, was deep fat fried in vegetable oil for 12 min at 135°C to an approximate internal temperature of 71°C. Three 2.54 cm cores were removed from the steak and the force (kg) required to shear the cores was measured using a Warner-Bratzler shear device. In summary, a total of eleven postweaning growth, carcass

composition and meat quality traits were potentially available on all steers. Records were not removed on the basis of missing observations, however, records were removed if pedigree information (sire and dam identification) was not available.

Analysis of Data. All possible pairwise comparisons among traits were made using the MTDFREML (Multiple Trait Derivative Free Maximum Likelihood) programs described by Boldman et al. (1995). Parameters of interest included additive genetic and phenotypic (co)variances from which phenotypic and genetic correlations were calculated. A two-trait animal model was fit for all trait pairs of the form:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & \\ & X_2 \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix} + \begin{bmatrix} Z_1 & \\ & Z_2 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

where

y = vector of observations for traits 1 and 2,

X_1 = known incidence matrix relating fixed effects to observations for trait 1,

X_2 = known incidence matrix relating fixed effects to observations for trait 2,

Z_1 = known matrix relating random effects to observations for trait 1,

Z_2 = known matrix relating random effects to observations for trait 2,

β_1, β_2 = unknown vector of fixed effects solutions for traits 1 and 2,

u_1, u_2 = unknown vector of random effects solutions for traits 1 and 2 and

e = vector of random residual terms unique to each observation.

Non-zero genetic and phenotypic (co)variances were allowed to arise as a result of relatedness among traits. Henderson (1984) explicitly described the mixed-model equations (MME) resulting from this model for animal applications as

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z + G^{-1} \end{bmatrix} \begin{bmatrix} b \\ u \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}$$

For N animals with t traits having the same fixed and random effects design (G* and R*) matrices, the model may be written as:

$$y = (I_t \times X) \beta + (I_t \times Z) U + e$$

The properties of the fixed and random effects solutions, denoted b and u, are summarized as:

$$E \begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} X\beta \\ 0 \\ 0 \end{bmatrix}$$

and

$$var \begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} V & ZG & R \\ GZ' & G & 0 \\ R & 0 & R \end{bmatrix}$$

where $V = var(y) = Z G Z' + R$ and $G = var(u) = A \otimes G_0$ with G_0 being the variance-covariance matrix of additive genetic animal effects. The matrix A is the additive relationship matrix for animals, computed using the full pedigree. The inverse of matrix G, $G^{-1} = A^{-1} \otimes G_0^{-1}$ is computed using the rules of Henderson and Quaas (1976). R is the variance-covariance matrix for random residuals. $R = diag \{R_i\}$, $i = 1, ..., N$ where R_i is a $t \times t$ matrix of residual (co)variances for progeny i. If R_0 denotes the residual variance-covariance matrix for a progeny with both traits recorded, R_i for animals with missing records can be formed from R_0 by substituting missing values with zero into the rows and columns of R_0 corresponding to the missing data. Henderson et al. (1959) showed that the b from the MME are best linear unbiased estimators (BLUE) of fixed effects as from generalized least-squares and Henderson (1963) proved that the u are best linear unbiased predictors (BLUP) of the random effects.

Incidence matrices for fixed effects were identical for all pairwise 2-trait analyses. All records were adjusted in the model with covariates corresponding to age of dam (yr), julian birth date (d) and slaughter age (d). Year was included in the model as a fixed effect. Direct and maternal additive genetic effects were fit as a series of eight covariates corresponding to the breed composition fractions for each steer and its dam. Direct and maternal heterosis were defined as the fraction of total breed heterozygosity in steers and dams of steers. Four direct heterosis coefficients were included in the

model which corresponded to the expected heterozygosity due to English x English (Angus x Hereford and Hereford x Angus), English (Angus or Hereford) x Brahman, English (Angus or Hereford) x Charolais and Brahman x Charolais breed interactions, denoted DEEH, DEBH, DECH and DBCH, respectively. The total maternal heterosis coefficient included in the model corresponded to total expected breed heterozygosity in the dam. The direct and maternal additive and non-additive genetic effects coefficients were obtained using the CANAGE (Coefficients for Additive and Non-additive Genetic Effects) programs of Gould and Crews (1996). Contrasts of direct and maternal additive and non-additive breed effects, referred to as direct and maternal genetic and heterosis effects, were obtained in the single trait analyses discussed previously. Random effects in the model included the usual genetic effect of animal and residual effects unique to observations. To maintain full rank in the coefficient matrix, C, of the MME, the direct and maternal additive Brahman solutions were set to zero.

The MTDFRUN component of the MTDFREML programs, performs the restricted maximum likelihood estimation which involves maximization of the log of the likelihood function (Λ) of the data which is independent of any fixed effects and includes a nonlinear function of the (co)variance components. The values of the (co)variances within the allowable parameter space which maximize Λ, or equivalently minimize -2Λ, are the REML estimates. Most REML algorithms commonly used in animal breeding research are gradient

of these gradient-type algorithms is that they require inversion of the left hand sides of the MME. The simplex method, which does not involve derivatives directly, is a geometric figure formed by a set of n + 1 points in n-dimensional space. The simplex employed in MTDFREML is formed by generating a new point to replace the worst, i.e., the point with the largest function value, so the simplex gradually moves "downhill" through the parameter space toward a minimum for -2Λ (Boldman et al., 1995). In these analyses, convergence (the stopping point) was defined at the point where the variance of the log-likelihood, var (-2Λ) < 1.00×10^{-6}. In all two-trait cases, convergence was reached within 500 rounds of iteration.

Results and Discussion

Components of variance are those as presented in Chapter 4, and therefore will not be repeated here. Additive genetic and phenotypic covariances among postweaning growth traits are presented in table 5.1 and corresponding genetic and phenotypic correlations are presented in table 5.2. Additive genetic and phenotypic covariances for all pairwise comparisons among carcass composition and meat quality traits are presented in table 5.3. Additive genetic and phenotypic correlations among carcass composition and meat quality traits are presented in table 5.4. In this chapter, covariances and correlations between postweaning and carcass traits will be presented separately.

Table 5.1 Estimates of Additive Genetic and Phenotypic Covariances Among Postweaning Growth Traits[a].

	RDG	FDG	SWT
RDG		0.01533	5.0106
FDG	0.00464		5.5413
SWT	1.1705	1.2789	

a Additive genetic covariances are in the lower triangle, phenotypic covariances are in the upper triangle.

Table 5.2 Estimates of Genetic (Rg) and Phenotypic (Rp) Correlations Among Postweaning Growth Traits[a].

	RDG	FDG	SWT
RDG		0.333	0.619
FDG	0.920		0.548
SWT	0.997	0.523	

a Genetic correlations are in the lower triangle, and phenotypic correlations are in the upper triangle.

Table 5.3 Estimates of Additive Genetic and Phenotypic Covariances for Carcass Composition and Meat Quality Traits[a].

	HCW	FAT	REA	WAR	FYG	TLY	MAR	WBS
HCW		3.6066	112.241	-41.275	6.6709	388.988	6.2098	-9.7093
FAT	-.0696		-0.1581	-0.4063	0.1735	0.7435	0.0815	-0.0317
REA	50.226	-0.5336		17.746	-2.492	74.8283	0.3715	-3.1093
WAR	-10.794	-0.2062	10.197		-1.5428	-11.843	-0.4786	-0.0753
FYG	-0.2719	0.0528	-2.013	-0.7316		0.9237	0.1422	0.0193
TLY	146.225	-0.4425	41.979	-2.8496	-1.068		2.3113	-5.2106
MAR	0.5024	0.0196	-0.4270	-0.1750	0.0338	-0.0385		-0.2111
WBS	-2.237	0.0328	-3.9212	-1.0930	0.1804	-2.6239	0.0601	

a Additive genetic covariances in the lower triangle, phenotypic covariances in the upper triangle.

Table 5.4 Estimates of Genetic (Rg) and Phenotypic (Rp) Correlations Among Carcass Composition and Meat Quality Traits[a].

	HCW	FAT	REA	WAR	FYG	TLY	MAR	WBS
HCW		0.350	0.435	-0.434	0.368	0.951	0.281	-0.145
FAT	-0.024		-0.049	-0.347	0.778	0.148	0.299	-0.038
REA	0.466	-0.459		0.606	-0.447	0.595	0.055	-0.151
WAR	-0.270	-0.526	0.711		-0.751	-0.250	-0.191	-0.010
FYG	-0.044	0.788	-0.821	-0.885		0.105	0.298	0.013
TLY	0.910	-0.251	0.662	-0.133	-0.292		0.214	-0.159
MAR	0.084	0.304	-0.180	-0.219	0.247	-0.011		-0.119
WBS	-0.148	0.201	-0.658	-0.544	0.525	-0.295	0.061	

a Genetic correlations are in the lower triangle and phenotypic correlations are in the upper triangle.

Phenotypic Correlations. Phenotypic correlations among postweaning growth traits were generally high and all were positive. Of interest was the phenotypic association between FDG and RDG. The estimate of this parameter in these data was Rp = 0.333 indicating a moderate to high and positive phenotypic association between gain on forage and gain on concentrate feed. RDG and FDG were both highly positively correlated with SWT (Rp = 0.619 and Rp = 0.548, respectively), which was expected since increased gain is expected to result in heavier weights at later ages.

Phenotypic correlations between HCW and other carcass composition and meat quality traits were generally moderate to high in magnitude. HCW tended to be most highly positively correlated with measures associated with total yield (REA and TLY). The phenotypic correlation between HCW and TLY was near unity (Rp = 0.951). Koch (1978) and Koch et al. (1982) found that the phenotypic correlation between HCW and retail product weight was 0.84. Moderately positive phenotypic relationships were observed between HCW and FAT and MAR. These results were in agreement with the work of Lamb et al. (1990) and Wilson et al. (1993) who reported moderately positive phenotypic correlations between HCW and FAT (Rp = 0.38 and 0.24, respectively). Also, Lamb et al (1990) and Veseth et al. (1993) reported a phenotypic correlation of 0.28 between HCW and MAR. The estimate of Wilson et al. (1993) was lower (Rp = 0.08). The moderately large negative phenotypic correlation between HCW and WAR (Rp = -0.434) indicated that heavier

carcasses were those with smaller weight adjusted ribeye areas. The moderately negative phenotypic correlation between HCW and WBS indicated a desirable relationship between increased HCW and tenderness as measured by WBS. Koch et al. (1982) reported a phenotypic correlation between HCW and WBS of zero.

The phenotypic correlation between FAT and REA and between FAT and WBS were near zero. Previous studies have reported this parameter to be negative (Koch, 1978; Koch et al., 1982; Wilson et al., 1993); however, the magnitude of these correlations were small. Lamb et al. (1990) reported that the phenotypic correlation between FAT and REA was 0.04. Koch et al. (1982) found that the phenotypic correlation between FAT and WBS was favorable (Rp = -0.01) but this estimate was also near zero. Conversely, FAT was moderately and negatively correlated with WAR. The positive association between HCW and FAT would tend to make the negative association between FAT and WAR expected. The phenotypic correlation of FAT with FYG was, as expected, very highly positive. These results support the findings of other researchers who have reported positive phenotypic correlations between FAT and FYG, or estimated percent retail yield (Koch et al., 1982). Likewise, FAT was positively associated with MAR (Rp = 0.299). Phenotypic correlation estimates of 0.12 to 0.38 have been reported between FAT and MAR (Koch, 1978; Koch et al., 1982; Lamb et al., 1990; Wilson et al., 1993).

Phenotypic measures of association between REA and other carcass traits were mostly converse to the corresponding associations with WAR. The exception to this general trend was that both REA and WAR had negative phenotypic correlations with FYG. It is easy to predict that REA would have a negative correlation with FYG based on the USDA yield grade equation. A negative phenotypic correlation between REA and FYG was reported by Koch et al. (1982). Likewise, it is intuitive that increases in carcass weight adjusted ribeye area would be negatively correlated with FYG. These negative correlations clearly show the desirable relationships between increases in muscling and increases in estimated carcass yield. However, the phenotypic correlation between WAR and TLY was negative, probably due partially to the negative relationship between HCW and WAR. Phenotypic correlations between REA and MAR and REA and WBS were smaller in magnitude, suggesting that little relationship exists between muscle size and carcass quality. Van Vleck et al. (1992) reported that phenotypic correlations between REA, WBS and sensory panel tenderness were near zero (Rp = -0.05 and zero, respectively). Estimated total lean yield (TLY) had desirable phenotypic associations with carcass quality. Koch et al. (1982) reported a near zero phenotypic correlation between retail product weight and WBS; however, the data of Koch and coworkers included actual retail yield rather than estimated yield. Since TLY had a high positive correlation with HCW, the correlations of TLY with other carcass traits was expected to be similar.

Genetic Correlations. Postweaning growth traits showed high and positive genetic correlations (table 5.2). The genetic correlation of RDG with FDG was estimated at Rg = 0.920 and with SWT at Rg = 0.997 indicating genetic relationships near unity. Similarly, the genetic correlation between FDG and SWT was high and positive (Rg = 0.523). These results indicate that in the evaluation of postweaning growth traits, rate of gain may be highly repeatable regardless of diet. And, as expected, higher breeding values for gain would be associated with higher breeding values for weight at slaughter.

The genetic correlation of HCW with REA and TLY (Rg = 0.466 and 0.910, respectively) supports the hypothesis that similar genes control weight and muscle size (table 5.4). Lamb et al. (1990) and Veseth et al. (1993) likewise reported high genetic correlations between HCW and REA, but the estimates of other researchers were lower (Koch, 1978; Koch et al., 1982; Wilson et al., 1993). Genetic correlations between HCW and FAT and between HCW and MAR were near zero. This was in agreement with the work of Koch et al., (1982) who also reported that the genetic correlation between HCW and FAT was 0.08. However, Koch (1978), Lamb et al. (1990) and Wilson et al. (1993) found higher positive genetic correlations between HCW and FAT. Literature estimates of the genetic correlation between HCW and MAR are highly variable, ranging from moderately negative to highly positive. Wilson et al. (1993) estimated the genetic correlation between HCW and MAR to be -0.06, however, the estimates of Koch et al. (1982), Veseth

et al. (1993) and Lamb et al. (1990) were positive. Koch (1978) reported that the genetic correlation between HCW and MAR was -0.33. Similar to the phenotypic correlation, the genetic correlation of HCW with WAR was moderately negative. The genetic correlation between HCW and WBS was low and negative (Rg = -0.148). Koch et al. (1982) estimated the genetic correlation between HCW and WBS to be zero.

Estimates of genetic correlations involving FAT were, in some cases, of greater magnitude than those involving HCW. The genetic correlations of FAT were generally negative with carcass composition traits associated with weight and yield, and positive with meat quality traits. The genetic correlation between FAT and FYG was largest (Rg = 0.788). FAT had highly negative genetic correlations with REA and WAR (Rg = -0.459 and -0.526, respectively). Koch et al. (1982), Lamb et al. (1990) and Wilson et al. (1993) also reported negative genetic correlations between FAT and REA, but Koch (1978) reported a near zero estimate of 0.03 for the genetic correlation between FAT and REA. FAT had moderately positive genetic correlations with MAR and WBS (Rg = 0.304 and 0.201, respectively). Most reports in the literature also reported the genetic correlation between FAT and MAR to be positive (Koch, 1978; Koch et al., 1982; Lamb et al., 1990). However, Wilson et al. (1993) found a negative genetic correlation between FAT and MAR (Rg = -0.13). Koch et al. (1982) and Van Vleck et al. (1992) found negative genetic correlations between FAT and WBS, different in sign to the

estimates found here. Similarly, Van Vleck et al. (1992) reported a positive genetic correlation of 0.74 between FAT and sensory panel tenderness.

Similar to the phenotypic correlation between REA and WAR, which was positive, the corresponding genetic correlation was highly positive. REA tended to have high and favorable genetic correlations with FYG, TLY and WBS; however, the genetic correlation between REA and MAR (Rg = -0.180) was not favorable. Koch et al. (1982) reported a genetic correlation between REA and retail product weight of 0.72. Most researchers have reported negative genetic correlations between REA and MAR (Koch, 1978; Koch et al., 1982; Van Vleck et al., 1992; Wilson et al., 1993); however, Lamb et al. (1990) and Veseth et al. (1993) reported estimates of 0.57 and 0.51 for the genetic correlation between REA and MAR. The genetic correlations between WAR and FYG, TLY, MAR and WBS were negative.

As expected, FYG and TLY had a genetic correlation that was moderately negative (Rg = -0.292) and FYG had positive genetic correlations with both MAR and WBS (Rg = 0.247 and 0.525, respectively). These results were in agreement with the findings of Koch et al. (1982) who found a genetic correlation of 0.46 between estimated cutability and retail product weight and a genetic correlation of -0.92 between estimated cutability and fat trim weight. Likewise, Koch et al. (1982) reported a large genetic correlation of -0.98 between estimated cutability and fat trim percentage.

Of particular interest in these analyses was the genetic correlation between MAR and WBS. The estimated genetic correlation between these traits was positive, indicating a tendency toward an undesirable relationship between marbling and tenderness, however, the value of the correlation (Rg = 0.061) was probably not different from zero. Koch et al. (1982) and Van Vleck et al. (1992) found moderately negative, and therefore favorable, genetic correlations between MAR and WBS. The estimate of Koch and coworkers was -0.25 and that of Van Vleck and coworkers was -0.53. Also, Shackleford et al. (1994) reported a genetic correlation of -0.57 between intramuscular fat content and WBS, further indicating a favorable association between marbling and tenderness. Further, Van Vleck et al. (1994) reported a genetic correlation of 0.74 between marbling score and sensory panel tenderness. Marshall (1994) summarized twelve genetic studies, and reported that marbling seemed to have a positive, although relatively weak association with palatability. He added that genetic correlations of WBS with other carcass traits were either favorable or near zero, indicating that selection for improved WBS, assuming it was practical, would be compatible to selection for improvement in other carcass traits, and that a genetic antagonism does not preclude simultaneous improvement in two traits.

Carcass Composition and Postweaning Growth Traits. Variance components for postweaning growth traits have been presented previously. Additive genetic and phenotypic covariances among postweaning growth and

carcass traits are given in tables 5.5, 5.6 and 5.7. Genetic (Rg) and phenotypic (Rp) correlations are presented in tables 5.8, 5.9 and 5.10.

Phenotypic Correlations. Daily gain on ryegrass (RDG) had high phenotypic correlations with HCW, REA and TLY (Rp = 0.657, 0.887 and 0.592, respectively). Moderate to high were the phenotypic correlations between RDG and FAT (Rp = 0.379), RDG and FYG (Rp = 0.406) and RDG and MAR (Rp = 0.418). A moderately negative phenotypic correlation was estimated between RDG and WAR (Rp = -0.338) indicating that faster gaining steers on ryegrass had less carcass weight adjusted ribeye area. The phenotypic correlation between RDG and WBS (Rp = -0.153) was also negative and indicative of a favorable phenotypic relationship between gain on ryegrass and tenderness, but the magnitude of this correlation was small. Phenotypic correlations between feedlot daily gain (FDG) and carcass traits showed a similar trend to those of RDG. This result was expected due to the high phenotypic and genetic correlations between FDG and RDG. FDG had highest phenotypic correlations with carcass measures of weight (HCW, TLY). The phenotypic correlation between FDG and WAR and between FDG and WBS were negative, similar to those with RDG, but were weaker in magnitude. These results support the favorable association between gain and tenderness but also indicate that increased gain was associated with decreased carcass weight adjusted ribeye area. The phenotypic correlations of FDG with FAT and MAR were low. The positive and small to moderate phenotypic correlation

Table 5.5 Estimates of Additive Genetic and Phenotypic Covariances Between Ryegrass Daily Gain (RDG) and Carcass Composition and Meat Quality Traits.

	RDG	
Trait	Additive genetic covariance	Phenotypic covariance
HCW	0.6179	3.6584
FAT	-0.0022	0.0259
REA	0.1315	1.5198
WAR	-0.0108	-0.2134
FYG	-0.0043	0.0489
TLY	0.4114	1.6070
MAR	0.0009	0.0613
WBS	-0.0081	-0.0682

Table 5.6 Estimates of Additive Genetic and Phenotypic Covariances Between Feedlot Daily Gain (FDG) and Carcass Composition and Meat Quality Traits.

	FDG	
Trait	Additive genetic covariance	Phenotypic covariance
HCW	1.1177	3.0714
FAT	0.0066	0.0109
REA	0.2673	0.4447
WAR	-0.0158	-0.1449
FYG	0.0043	0.0176
TLY	0.6478	1.5006
MAR	0.0097	0.0134
WBS	0.0019	-0.0578

Table 5.7 Estimates of Additive Genetic and Phenotypic Covariances Between Slaughter Weight (SWT) and Carcass Composition and Meat Quality Traits.

	SWT	
Trait	Additive genetic covariance	Phenotypic covariance
HCW	378.743	1113.08
FAT	0.2129	4.0823
REA	77.829	141.949
WAR	-15.230	-58.107
FYG	-0.1794	8.3071
TLY	218.235	524.75
MAR	1.6473	6.6579
WBS	-0.2182	-10.052

Table 5.8 Estimates of Genetic (Rg) and Phenotypic (Rp) correlations Between Ryegrass Daily Gain (RDG) and Carcass Composition and Meat Quality Traits.

	RDG	
Trait	Genetic correlation	Phenotypic correlation
HCW	0.759	0.657
FAT	-0.249	0.379
REA	0.409	0.887
WAR	-0.100	-0.338
FYG	-0.233	0.406
TLY	0.860	0.592
MAR	0.049	0.418
WBS	-0.180	-0.153

Table 5.9 Estimates of Genetic (Rg) and Phenotypic (Rp) Correlations Between Feedlot Daily Gain (FDG) and Carcass Composition and Meat Quality Traits.

	FDG	
Trait	Genetic correlation	Phenotypic correlation
HCW	0.660	0.442
FAT	0.360	0.128
REA	0.401	0.208
WAR	-0.070	-0.184
FYG	0.113	0.117
TLY	0.650	0.443
MAR	0.258	0.073
WBS	0.023	-0.104

Table 5.10 Estimates of Genetic (Rg) and Phenotypic (Rp) Correlations Between Slaughter Weight (SWT) and Carcass Composition and Meat Quality Traits.

	SWT	
Trait	Genetic correlation	Phenotypic correlation
HCW	0.957	0.912
FAT	0.050	0.272
REA	0.505	0.378
WAR	-0.289	-0.420
FYG	-0.017	0.315
TLY	0.938	0.882
MAR	0.189	0.207
WBS	-0.010	-0.103

between FDG and FYG was expected due to the associations of FDG with HCW and FAT since increases in carcass weight and fatness are expected to result in higher yield grades. Koch (1978), Koch et al. (1982), Lamb et al. (1990) and Veseth et al. (1993) similarly found high phenotypic and genetic correlations between postweaning average daily gain and hot carcass weight. These researchers also found moderately positive phenotypic and genetic correlations between postweaning average daily gain and REA. However, Koch (1978) reported a genetic correlation of -0.07 between postweaning average daily gain and REA. Fat thickness had positive phenotypic and genetic correlations with postweaning average daily gain in the study of Koch (1978), Koch et al. (1982) and Lamb et al. (1990), but MacNeil et al. (1984) reported a genetic correlation of -0.20 between postweaning average daily gain and FAT. Koch et al. (1982), Lamb et al. (1990) and Veseth et al. (1993) reported positive phenotypic correlations between postweaning daily gain and MAR, but the corresponding genetic correlations were smaller and in some cases near zero. Koch (1978) reported a negative genetic correlation between postweaning gain and MAR (Rg = -0.62). Shackelford et al. (1994) reported high and positive phenotypic and genetic correlations between feedlot daily gain and retail product weight (Rp = 0.74; Rg = 0.92). Koch et al. (1982) reported near zero phenotypic and genetic correlations between postweaning gain and WBS, but Shackelford et al. (1994) found these estimates to be moderate and negative. Shackelford and coworkers concluded that selection

for increased growth rate during feeding would be favorably associated with positive responses in tenderness.

The phenotypic correlation between SWT and HCW (Rp = 0.912) indicated that these two traits were essentially the same. SWT also had highly positive phenotypic correlations with REA and TLY. Also positive but moderate in magnitude were the correlations of SWT with FAT, FYG and MAR. Again, SWT had negative phenotypic correlations with WAR and WBS.

The association between SWT and WBS was small (Rp = -0.103), but still supports the overall trend in these data for increased performance (weights and gains) to be favorably associated with tenderness. However, the same increases in performance were also associated with decreased WAR. The positive phenotypic correlations of postweaning growth traits with FYG further indicate that increases in weight at any age will have negative impact on carcass yield. Shackelford et al. (1994) reported that increased gain in the feedlot had favorable relationships with total lean yield and tenderness, and concluded that selection for increased growth would be expected to have favorable correlated response in yield and tenderness.

Genetic Correlations. Genetic correlations of RDG with HCW and TLY were high and positive, similar in magnitude and sign to the corresponding phenotypic correlations. Also, the genetic correlation between RDG and WBS was negative but small. The moderately negative phenotypic correlation between RDG and WAR corresponded to a weaker but still negative genetic

correlation. Also, the genetic correlation between RDG and MAR was weaker but similar in sign to the corresponding phenotypic correlation. Of particular interest was that although the phenotypic correlation between RDG and FAT was moderate and positive, the corresponding genetic correlation was negative and moderate. These results indicate that although increased gain on ryegrass had a positive phenotypic effect on FAT, the genetic control of RDG did not have a positive effect on FAT. These results are consistent with the assumption that increased RDG would be more associated with lean growth and its associated weight gain rather than fattening. Similarly, although the phenotypic correlation between RDG and FYG was positive, the genetic correlation was negative. This further indicates that selection for RDG would have a favorable effect on FYG.

Genetic correlations between FDG and carcass traits were positive with the exception of that with WAR, which was negative but near zero. Since RDG had a negative genetic correlation with FAT and FDG had a positive genetic correlation with FAT, it is assumed that increased feedlot performance tended to be more associated with increases in FAT than was increased RDG. FDG had highly positive genetic correlations again with HCW, REA and TLY. The moderately positive genetic correlation between FDG and MAR (Rg = 0.258) was assumed also to be related with fattening. Comparison of genetic correlation trends between RDG and FDG may lead to the conclusion that

selection for increased RDG may have less unfavorable impact on carcass composition than selection for increased FDG. Similar to RDG and FDG, the genetic correlations of SWT with HCW and TLY were positive and near unity (Rg = 0.957 and Rg = 0.938, respectively).

These data consistently supported the hypothesis that weights and total yield are highly correlated in terms of genetic control. However, these results also indicate a trend that increases in weights are also associated with decreases in carcass weight adjusted ribeye, leading ultimately to unfavorable relationships with FYG. However, since it is probable that increased TLY is a better indicator of saleable yield than is FYG, these genetic relationships might still be considered favorable. It is important to note that FYG is an estimate of percentage yield unlike TLY, and increased FYG still indicates lower yield among carcasses of similar weight. Finally, the genetic relationships of SWT with carcass quality (MAR and WBS) were favorable; however, the strength in general of the genetic relationships between postweaning growth and carcass quality were not high.

CHAPTER 6

GENETIC AND PHENOTYPIC CORRELATIONS BETWEEN PREWEANING AND CARCASS TRAITS AMONG BRAHMAN-INFLUENCED BEEF STEERS (PHASE II)

Introduction

There has been an increase in the frequency of scientific literature reporting genetic parameters for traits associated with postweaning growth, carcass composition and meat quality. Few studies, however, have focused on phenotypic and genetic associations between traits associated with preweaning performance and postweaning performance or carcass composition. These relationships could be important in the design of mating systems and in the selection of cattle.

The importance of carcass traits in the beef industry has been widely recognized. There is an insufficient amount of carcass data which can be traced to genetic origin (NCA, 1992). As the beef industry continues toward a value-based marketing system, selection programs must be designed which optimize carcass composition, but also consider relationships between measures of carcass merit and early-life traits. Also, evaluating the additive genetic merit of potential parents could be improved if early-life indicators of carcass merit were identified.

It has long been established that the relationships among traits of economic importance may slow total genetic progress with regard to the highly segmented phases of the beef industry. That is, selection for preweaning

performance to improve profitability of the cow herd in the beef industry may have negative correlated responses among carcass traits deemed important to the profitability of the feeding and packing segments. Also, the genetic relationships between carcass traits and reproductive traits in relative females have been estimated in only a few cases.

The objective of the present study was to estimate phenotypic and genetic correlations between preweaning performance and carcass traits for steers produced in a multi-generation crossbreeding study.

Materials and Methods

Data Collection and Cattle Management. Data on preweaning and carcass measures were available from steers (N = 1530) produced from 1970 to 1988 in a multi-generation crossbreeding study involving the Angus, Brahman, Charolais and Hereford breeds conducted at the Louisiana State University Agricultural Center Ben Hur Crossbred Beef Cattle Research Unit in Baton Rouge. The environment is subtropical with average minimum and maximum daily temperatures of 13 and 26°C, average minimum and maximum humidity of 54 and 88%, and average annual rainfall of 147 cm.

Purebred bulls representing the Angus, Brahman, Charolais and Hereford breeds were mated to straightbred and crossbred cows to produce straightbred, F_1, back-cross, three-breed cross and 2-, 3- and 4-breed rotational crossbred calves. The crossbred mating system was designed such that generations were non-overlapping and that all crossbred calves contain

some percentage Brahman breeding. A detailed comparison of generations and mating systems with respect to carcass traits is given by DeRouen et al. (1992). Variance components and mating systems analyses for preweaning traits have been reported by Salgado (1995).

Calves were born during spring calving seasons between mid-January and mid-April of each year, and were weighed and identified at birth. Bull calves were castrated at approximately 135 d of age, and then weaned during the first week of October at approximately 220 d of age. Preweaning performance data available included birth weight (BWT), average daily gain during the preweaning period (PDG) and adjusted 205-d weaning weight (WWT).

Following weaning, steers were placed on a backgrounding program for approximately 60 d. Following backgrounding, steers were placed on a forage-based stocker program for approximately 150 d during which, the steers grazed annual ryegrass (*Lolium multiflorum*) prior to being placed in the feedlot. Following the stocker phase, steers were placed in the feedlot and fed a high energy corn-based diet for a period ranging from 0 to 200 d. A few steers were placed on feed following weaning, and some were slaughtered directly off ryegrass. Age at slaughter was calculated for each steer.

At the end of feeding, steers were slaughtered and processed and carcass data were obtained. Carcass composition trait measures available included hot carcass weight (HCW), fat thickness opposite the longissimus

muscle at the 12-13th rib interface (FAT) and area of the exposed face of the longissimus muscle at the 12-13th rib interface (REA). Carcass weight adjusted ribeye area (WAR), USDA yield grade (FYG) and estimated carcass total lean yield (TLY) were also calculated (USDA, 1989). Meat quality traits included USDA marbling score (MAR) and Warner-Bratzler shear force (WBS). The procedure for obtaining WBS, a measure of tenderness, involved removing a 3.8 cm thick longissimus steak from the 12th rib region of the right side of the carcass. After 7 d of aging, the steak was deep-fat fried in vegetable oil for 12 min and 135°C to an approximate internal temperature of 71°C. Three 2.54 cm cores were removed from the steak and the force (kg) required to shear the core was measured using a Warner-Bratzler shear device.

Data Analysis. Data were analyzed using the Multiple Trait Derivative Free Maximum Likelihood (MTDFREML) programs of Boldman et al. (1995). In summary, three preweaning and eight carcass composition and meat quality traits were available, resulting in 24 pairwise (2-trait) analyses, with a maximum of 1530 observations for each of the eleven traits. The variance components for carcass composition and meat quality traits (additive genetic and residual variances) were estimated in previous analyses, therefore, only covariances were of interest in this study. The variance components for preweaning traits, however, will be summarized. Estimates of fixed effects will not be repeated here. Data editing consisted of removal of all records from the data which did not have complete pedigree and breed composition

information. Warner-Bratzler shear values were not available for the later generations, therefore, only 863 WBS observations were used in these analyses. For each of the remaining traits, a maximum of 1530 observations were available.

For each pairwise analysis, data were fit using a two-trait animal model of the general form:

$$y = X\beta + Z\,U + Wd + e$$

where

y = the vector of observations

X = the known design matrix relating fixed effects to observations,

β = the unknown vector of fixed effects solutions,

Z = the known matrix relating random (genetic) effects to observations,

U = the unknown vector of random effects solutions

W = the known matrix relating total maternal (G + PE) effects to observations,

d = the unknown vector of total maternal effects solutions and

e = the unknown vector of random residuals unique to observations.

Henderson's mixed model equations (MME) simplify the calculation of the estimators of β, U and d, denoted b, u and d, for this model. Fixed effects included covariates corresponding to age of dam (yr), julian birth date of steer (d) and slaughter age of steer (d). Year of birth was also included as a fixed effect. Direct and maternal additive and non-additive breed effects were fit using coefficients corresponding to the additive breed composition of steers

and dams of steers and to the expected breed heterozygosity in steers and dams of steers. Four direct heterosis coefficients for steers were calculated corresponding to expected fractions of English x English (DEEH), English x Brahman (DEBH), English x Charolais (DECH) and Brahman x Charolais (DBCH) breed heterozygosity. The maternal heterosis coefficient was the sum of all unlike breed x breed interactions from the additive breed composition of the dam. Coefficients for direct and maternal additive and non-additive genetic effects were obtained using the CANAGE programs of Gould and Crews (1996). Estimates and contrasts of direct and maternal breed and heterosis effects were discussed previously for carcass traits. A detailed discussion of fixed effects on preweaning traits for these data was presented by Salgado (1995) and Habet (1996). Three likelihood ratio tests were conducted to test the hypothesis that maternal effects were important for traits in the final models. For the three preweaning traits, a full model containing a total maternal (maternal genetic plus permanent environmental variance) component in addition to additive (animal) effects was fit. The likelihood of the full model for each trait was compared to the reduced model containing only additive genetic effects. The difference in likelihoods was assumed to be distributed as chi-square with degrees of freedom equal to the difference in the number of parameters between the two models. In this case, the degrees of freedom for the chi-square tests of significance were one for all likelihood ratio tests.

The MTDFREML programs evaluate the log likelihood (-2Λ) and iteratively locate the minimum using the simplex algorithm (Boldman et al., 1995). For these analyses, convergence was attained at the point when the variance of the log likelihood, $V(-2\Lambda) < 1.00 \times 10^{-6}$. Convergence criteria were met in all analyses within 500 rounds of iteration. A minimum of three cold restarts (Boldman et al., 1995) were conducted to ensure that the global rather than a local minimum for -2Λ had been found.

Results and Discussion

Sample summary statistics for preweaning growth traits are presented in Table 6.1. Table 6.2 summarizes three likelihood ratio tests of significance for the total maternal component of variance. Salgado (1995) showed that maternal effects were important for preweaning traits in these data. Likelihood ratio tests of significance for total maternal components of variance for carcass traits were not significant ($P > .05$) and will not be presented. However, likelihood comparisons models for all preweaning traits were significant ($P < .001$). Therefore, the final models for these analyses contained additive genetic and total maternal random terms for the preweaning traits, but only additive genetic effects for carcass traits.

The additive genetic, total maternal and phenotypic variances (table 6.3) indicated that preweaning traits had moderate heritabilities. Additive heritabilities were calculated as the ratio of additive genetic variance to the sum of additive plus residual variance. The additive heritability estimates for

Table 6.1 Summary Statistics for Preweaning Growth Traits.

Trait	N	MIN	MAX	AVG	STD
BWT, kg	1530	15.422	59.870	34.180	6.62
PDG,kg/d	1530	0.3700	1.500	0.8840	0.136
WWT, kg	1530	112.14	345.60	215.36	30.69

Table 6.2. Summary of Likelihood Ratio Tests for Preweaning Traits With Total Maternal Component of Variance.

	-2 Λ			
Preweaning trait	Full model	Reduced model	LRTS[a]	P[b]
BWT	6228.57	6251.49	22.92	.001
PDG	-5500.27	-5479.59	20.69	.001
WWT	10776.33	10797.50	21.17	.001

a Likelihood ratio test statistic
b $P = Pr(\chi^2_1 > LRT \mid H_0 \text{ is true})$

Table 6.3 Estimates of Additive Genetic, Total Maternal, Residual and Phenotypic Variances for Preweaning Growth Traits.

	Additive genetic variance	Total maternal variance	Residual variance	Phenotypic variance
BWT	7.171	5.384	10.405	22.960
PDG	0.00295	0.00178	0.00446	0.00919
WWT	137.526	99.874	228.055	465.455

Table 6.4 Estimates of Additive (h_a^2) and Total Maternal (h_t^2) Heritabilities for Preweaning GrowthTraits.

	Additive heritability	Total maternal heritability
BWT	0.312	0.547
PDG	0.321	0.515
WWT	0.295	0.510

preweaning traits were h^2 = 0.312 for BWT, h^2 = 0.321 for PDG and h^2 = 0.295 for WWT (table 6.4). Total maternal heritability (table 6.4) was defined as the ratio of additive plus total maternal variance to phenotypic variance. Since this calculation contains one additional numerator component of variance, total maternal heritability estimates were expected to be an upper bound to additive heritability estimates. Total maternal heritability, as discussed here, is analogous to repeatability, containing additive genetic, maternal genetic and permanent environmental components of variance (Van Vleck, 1992).

Additive genetic and phenotypic covariances between BWT, PDG and WWT and carcass traits are presented in tables 6.5, 6.6 and 6.7, respectively. Likewise, table 6.8 lists additive genetic (Rg) and phenotypic (Rp) correlations between preweaning and carcass traits. Phenotypic correlations between BWT and carcass traits were generally negative when carcass traits measured fatness (i.e., FAT, FYG, MAR). The phenotypic correlation between BWT and WBS was also negative. Although negative in sign, this correlation was close to zero (Rp = -0.024). The higher, positive phenotypic correlations involving BWT were with HCW (Rp = 0.385) and REA (Rp = 0.175).

Genetic correlations involving BWT were high and positive with HCW (Rg = 0.624) and REA (Rg = 0.347). The genetic correlation between BWT and TLY was positive (Rg = 0.622), further supporting the association between increased growth performance and estimated lean yield. The genetic

Table 6.5 Estimates of Additive Genetic and Phenotypic Covariances Between Birth Weight (BWT) and Carcass Composition and Meat Quality Traits.

	BWT	
Trait	Additive genetic covariance	Phenotypic covariance
HCW	27.615	53.441
FAT	-0.0229	-0.0435
REA	6.059	7.4741
WAR	-0.5656	-2.455
FYG	-0.0061	0.0899
TLY	16.199	27.337
MAR	-0.1216	-0.2520
WBS	-0.9887	-0.2664

Table 6.6 Estimates of Additive Genetic and Phenotypic Covariances Between Preweaning Average Daily Gain (PDG) and Caracass Composition and Meat Quality Traits.

	PDG	
Trait	Additive genetic covariance	Phenotypic covariance
HCW	0.6588	1.5774
FAT	0.0021	0.0034
REA	0.0974	0.2008
WAR	-0.0436	-0.0777
FYG	-0.0035	0.0076
TLY	0.3692	0.7676
MAR	-0.0007	-0.0008
WBS	-0.0073	-0.0133

Table 6.7 Estimates of Additive Genetic and Phenotypic Covariances Between 205-d Weaning Weight (WWT) and Carcass Composition and Meat Quality Traits.

	WWT	
Trait	Additive genetic covariance	Phenotypic covariance
HCW	151.557	213.927
FAT	0.4685	0.6763
REA	25.081	48.459
WAR	-9.520	18.491
FYG	0.5552	1.5935
TLY	84.510	183.406
MAR	-0.0298	-0.4118
WBS	-3.687	-2.9980

Table 6.8 Estimates of Genetic (Rg) and Phenotypic (Rp) Correlations Between Preweaning GrowthTraits and Carcass Composition and Meat Quality Traits.

	BWT		PDG		WWT	
Trait	Rg	Rp	Rg	Rp	Rg	Rp
HCW	0.624	0.385	0.734	0.568	0.782	0.600
FAT	-0.048	-0.026	0.218	0.099	0.224	0.088
REA	0.347	0.175	0.275	0.235	0.328	0.252
WAR	-0.096	-0.156	-0.365	-0.247	-0.369	-0.261
FYG	-0.006	0.030	0.172	0.127	0.126	0.118
TLY	0.622	0.404	0.699	0.567	0.741	0.602
MAR	-0.125	-0.069	-0.037	-0.011	-0.007	-0.025
WBS	-0.404	-0.024	-0.148	-0.060	-0.344	-0.060

correlation between BWT and MAR was moderately negative (Rg = -0.125) as was the genetic correlation between BWT and WBS (Rg = -0.404). The remainder of the carcass traits had genetic correlations with BWT that were near zero.

Additive genetic and phenotypic correlations between carcass traits and PDG are also listed in table 6.8. PDG was strongly and positively associated with HCW (Rp = 0.568 and Rg = 0.734) and with REA (Rp = 0.235 and Rg = 0.275). These results agreed with the findings of Koch (1978), Koch et al. (1982) and Veseth et al. (1993) who reported moderate and positive phenotypic correlations between preweaning average daily gain or weaning weight and HCW. Likewise, these researchers found moderate and positive phenotypic correlations between PDG and REA. Phenotypic correlations between PDG and FAT, FYG and MAR were close to zero. Lamb et al. (1990) reported a phenotypic correlation of 0.20 between PDG and FAT. The phenotypic correlation estimates of Koch (1978), Koch et al. (1982) and Woodward et al. (1992) for PDG and MAR were near zero as well. However, the genetic correlation between PDG and FAT was positive and moderate (Rg = 0.218). PDG and WAR were negatively correlated, both at the phenotypic level (Rp = -0.247) and the genetic level (Rg = -0.365). Both phenotypic and genetic correlations between PDG and MAR were small. Although the phenotypic correlation between PDG and WBS was near zero (Rp = -0.060), their genetic correlation was larger and negative (Rg = -0.148). Koch et al.

(1982) found near zero phenotypic and genetic correlations between preweaning average daily gain and WBS. It appeared that gain in the preweaning period was positively associated with carcass measures of weight and muscle size, negatively associated with total carcass muscle and not significantly correlated with carcass measures of fat or marbling. The moderately negative genetic correlation between PDG and WBS warrants further investigation.

Correlations between WWT and carcass traits tended to be larger in magnitude than those of BWT and PDG. Similar to BWT and PDG, WWT was negatively associated with WAR (Rp = -0.261 and Rg = -0.369) and WBS (Rp = -0.060 and Rg = -0.344). Koch et al. (1982) reported near zero phenotypic and genetic correlations between weaning weight or preweaning average daily gain and WBS. WWT was positively associated with HCW (Rp = 0.600 and Rg = 0.782) and REA (Rp = 0.252 and Rg = 0.328). This was in agreement with the results of Lamb et al. (1990) and Veseth et al. (1993) who also found moderate to large and positive correlations between weaning weight or preweaning gain and HCW and REA. The correlations between WWT and FAT were positive (Rp = 0.088 and Rg = 0.224) indicating that at weaning, heavier steers were also steers that were predisposed to fattening. Lamb et al. (1990) found that the phenotypic and genetic correlations between weaning weight and FAT were moderate and positive. WWT had moderate and positive associations with FYG (Rp =

0.118 and Rg = 0.126) and TLY (Rp = 0.741 and Rg = 0.602). This was in agreement with the work of Koch (1978) and Koch et al. (1982) who also reported positive phenotypic and genetic correlations between weaning weight and retail product weight. The phenotypic correlations of WWT with MAR and WBS were negative but near zero. Genetic correlations between WWT and carcass quality traits were also near zero with the exception of the genetic correlation between WWT and WBS, which was -0.344, indicating a favorable association between preweaning growth performance and tenderness. Shackelford et al. (1994) found negative and therefore favorable phenotypic and genetic correlations between rate of gain and calpastatin activity.

These analyses indicated that as steers approached weaning, phenotypic and genetic correlations between preweaing traits and carcass traits were generally stronger, although the signs were different, depending on the traits involved. Further study of these relationships is warranted. Of particular interest would be the phenotypic and genetic relationships among traits associated with carcass merit and traits associated with reproduction.

CHAPTER 7

HETEROGENEITY OF VARIANCE BY PERCENTAGE BRAHMAN INFLUENCE IN CARCASS COMPOSITION AND MEAT QUALITY TRAITS (PHASE II)

Introduction

Differences in variances among breeds of beef cattle have been of concern when procedures for crossbred or multibreed genetic evaluations have been proposed (Elzo and Famula, 1985; Arnold et al., 1992). Van Vleck (1994) pointed out that different variances for different sire breeds may not be very important for estimating sire breed mean differences required to obtain interbreed EPD, but differences in variances could be of consequence for the prediction of random genetic merit of a sire with respect to the mean of its breed. In addition, Van Vleck (1994) indicated that it could be necessary to consider differences in variances due to dam breeds.

Heterogeneity of variance can apply to residuals or other random effects in the model. Treating records of animals in subclasses with different variances as being different traits is a methodology that has been used to account for this heteroscedasity (Rodriguez-Almeida et al., 1995).

Rodriguez-Almeida et al. (1995) concluded that sire breed, sex and dam breed significantly contributed to heterogeneity of variance in 200- and 365-day weights in a multibreed population of beef cattle. They implied that the development of an animal model for multibreed genetic evaluation would require taking into account the differences in genetic and phenotypic variances

among breeds and sexes. The consideration of this heteroscedasity can be accomplished using a variant of the animal model. Further, Garrick et al. (1989) found that heterogeneity of variances in beef cattle can exist not only with respect to breed composition, but also according to the sex of the calf, which could result in reranking of animals to be selected if those differences were ignored, with the result that genetic progress could be slowed.

Analyses of the heterogeneity of variance problem in multibreed genetic evaluation of carcass traits have not been reported. As the importance of carcass merit continues to increase in beef cattle evaluation, it will be necessary to account for sources of variance heterogeneity in multibreed populations.

The majority of calves produced in the U.S. beef industry are produced from crossbred mating systems. The potential for reranking of sires in multiple trait analyses due to heterogeneity of variance should be considered. In planned crossbreeding programs where purebred sires are mated to both purebred and crossbred dams to produce calves of variable breed composition, models may be written which treat separately those traits which are observed in crossbred and straightbred calves differing in direct and maternal additive breed composition.

In the Gulf Coast Region of the U.S. beef industry, a large percentage of the cow herd and calves produced have some percentage Brahman influence. As percentage Brahman increased, some researchers have observed

increases in variability in traits (Mies, 1996). Studies of heteroscedasity due to percentage Brahman influence have not been reported in the literature.

The purpose of this study was to investigate the nature of heterogeneity of variance due to percentage Brahman influence in carcass traits of straightbred and crossbred calves produced in a multigeneration, multibreed crossbreeding study involving the Angus, Brahman, Charolais and Hereford breeds.

Materials and Methods

Description of Data. Carcass records on straightbred and crossbred steers (N = 1530) produced from 1970 - 1988 as part of a multi-generation crossbreeding study were available. Unselected purebred sires representing the Angus, Brahman, Charolais and Hereford breeds were mated to purebred and crossbred cows to produce straightbred, F_1, back-cross, three-breed cross, and 2-, 3- and 4-breed rotational crossbred calves. The mating system was designed such that generations were non-overlapping and that all crossbred calves contained some percentage Brahman. The environment at the Louisiana State University Agricultural Center Crossbred Beef Cattle Research Unit is subtropical with an average annual rainfall of 147 cm. Average daily minimum and maximum temperatures are 13 and 26°C and average daily minimum and maximum humidity are 54 and 88%.

All calves were born in spring calving seasons between mid-January and mid-April of each year and were weighed and identified at birth. Bull calves

were castrated at approximately 135 d of age and then weaned at approximately 220 d of age during the first week in October. Following weaning, steers were placed in a backgrounding program for 60 d followed by most steers being placed on a ryegrass-based stocker program for 150 d. Few steers were placed directly into the feedlot after backgrounding. During the feedlot phase, steers were fed a corn-based diet for a period ranging from 0 to 200 d, some steers being slaughtered at the end of the stocker period. Age at slaughter (d) was calculated for each steer.

Following routine slaughter and processing procedures, carcass yield traits were measured including hot carcass weight (HCW), subcutaneous fat thickness over the 12-13th rib (FAT) region and area of the exposed face of the longissimus muscle at the 12-13th rib (REA) region of the carcass. Final USDA yield grade (FYG), carcass weight adjusted ribeye area (WAR) and estimated total lean yield (TLY) were calculated from these data (USDA, 1989). Meat quality traits inciuded marbling score (MAR) and Warner-Bratzler shear force (WBS). The procedure for obtaining WBS involved removing a 3.8 cm thick longissimus steak from the 12th rib region, which, at d-7 postmortem, was deep-fat fried in vegetable oil for 12 min at 135°C to an approximate internal temperature of 71°C. Three 2.54 cm cores were removed from the steak and the force (kg) required to shear the core was measured using a Warner-Bratzler shear device.

Analysis of Data. Each of the eight carcass composition and meat quality traits were analyzed separately. To study heterogeneity of variance due to percentage Brahman influence, a multivariate animal model with records of steers scored as high (HB) or low percentage (LB) Brahman considered different traits, and with the same model equation but differing in covariance structure, was fit.

The model equations were:

$$\begin{bmatrix} y_{HB} \\ y_{LB} \end{bmatrix} = \begin{bmatrix} X_{HB} & 0 \\ 0 & X_{LB} \end{bmatrix} \begin{bmatrix} \beta_{HB} \\ \beta_{LB} \end{bmatrix} + \begin{bmatrix} Z_{HB} & 0 \\ 0 & Z_{LB} \end{bmatrix} \begin{bmatrix} U_{HB} \\ U_{LB} \end{bmatrix} + \begin{bmatrix} e_{HB} \\ e_{LB} \end{bmatrix}$$

Combining the equations can be summarized as:

$$y = X B + Z U + e$$

where the following definitions apply:

y = vector of observations corresponding to the level of Brahman influence

X = known incidence matrix relating fixed effects to observations

β = unknown vector of fixed effects solutions

Z = known incidence matrix relating random (genetic) effects to observations

U = unknown vector of random effects solutions, and

e = vector of random residuals unique to observations.

Variance-covariance structures for random effects and residuals can be written as the direct sums of submatrices corresponding to each sire breed:

$$var\begin{bmatrix} U_{HB} \\ U_{LB} \end{bmatrix} = \left(\begin{bmatrix} \sigma^2_{U_{HB}} & 1 \\ 1 & \sigma^2_{U_{LB}} \end{bmatrix} \right) = G$$

and

$$var\begin{bmatrix} e_{HB} \\ e_{LB} \end{bmatrix} = \left(\begin{bmatrix} \sigma^2_{e_{HB}} & 0 \\ 0 & \sigma^2_{e_{LB}} \end{bmatrix} \right) = R$$

Then, using the mixed model equations (MME) of Henderson (1984)

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z + G^{-1} \end{bmatrix} \begin{bmatrix} b \\ u \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}$$

with

$$E\begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} X\beta \\ 0 \\ 0 \end{bmatrix}$$

Variance components were estimated by a derivative-free REML simplex algorithm using the Multiple Trait Derivative Free Restricted Maximum Likelihood (MTDFREML) programs of Boldman et al. (1995). The procedure consists of iteratively locating variance components that minimize -2 times the restricted log likelihood function, that is,

$$-2\,\Lambda = \text{constant} + \log|R| + \log|G| + \log|C| + y'Py$$

where C is the full rank submatrix of the coefficient matrix for Henderson's MME and y'Py is the generalized residual sum of squares.

The model classified steers into low and high Brahman influence based on direct additive Brahman breed composition. Steers that were twenty five percent or more Brahman were classified HB, while those that were less than twenty five percent Brahman were classified LB. Direct and maternal additive and non-additive breed effects coefficients were generated using the CANAGE programs of Gould and Crews (1996) and were included in the fixed effects portion of the model to account for additive breed composition of steers and dams of steers. Covariates in the model adjusted steer records for year of birth, age of dam, julian birth date, age at slaughter, and fractions of total heterosis in steers and dams. To maintain full rank in the MME, the direct and maternal additive Brahman effects were constrained to a solution of zero. Convergence for these analyses was set at the point where the variance of the likelihood, var $(-2\Lambda) < 1.00 \times 10^{-6}$ and was attained within 300 rounds of iteration for all traits.

Each trait was analyzed separately. To study heterogeneity of variance due to percentage Brahman influence, two models were used. In the common variances model (COM), records of steers in the two percentage Brahman influence classifications were considered the same trait. This model was equivalent to the standard single trait model. (Co)variances were assumed to be the same for the two levels of Brahman influence in the COM model. Fixed

effects were fit for each level of year of birth. In the complete model (DIF), traits were considered different with regard to the two levels of Brahman influence with different (co)variances. This resulted in a two trait model. Comparisons were made between the two models with likelihood ratio tests. In the DIF model, genetic covariances were constrained to yield a genetic correlation of 1.00, and residual covariances were not fit.

Likelihood Ratio Tests. The likelihood ratio tests consisted of comparing the minimized value of -2Λ for the model with more parameters from the value of -2Λ corresponding to the model with fewer parameters (i.e., fewer parameters to estimate). The difference was compared with a chi-square distribution with degrees of freedom equal to the difference in the number of parameters estimated for the two models. The -2Λ values used for the common variances (COM) and complete (DIF) models were those obtained at convergence of the iterative process carried out by MTDFREML. Genetic covariances in the DIF models were held constant, and assumed to have a genetic correlation of 1.00. In the DIF models, the residual covariance was not fit. Because the log $|C|$ part of -2Λ depends on the constraints being imposed, when models with two traits (DIF) were compared to single trait models (COM) it was ensured that the models were equivalent with respect to the fixed effects part and the constraints were on the same equations for the common fixed effects of the pairs of models being compared. Exact probabilities satisfying the expression $P(\chi^2_{d.f.} > LRT \mid Ho \text{ is true})$, where LRTS

is the likelihood ratio test statistic, were computed using the SAS system (SAS, 1989). The null hypothesis to be tested was that variances were the same across HB and LB classifications.

Results and Discussion

Sample summary statistics for COM and DIF models are presented in table 7.1. For most carcass traits, the range of values for the HB classification were greater than the corresponding LB classification. Mies (1996) reported that increasing percentage Brahman influence was associated with larger ranges in traits related to carcass quality in the Texas Ranch to Rail carcass evaluation program. Further, Crews (1992) noted greater variability in carcass traits among steers with fifty versus less than fifty percent Brahman influence.

Results of comparisons of COM and DIF models are given in table 7.2. For all comparisons, the difference in likelihoods yielded a likelihood ratio test statistic (LRTS) which was assumed to be distributed as chi-square with three degrees of freedom. The degrees of freedom were calculated as the difference in number of parameters between DIF and COM models. Most likelihood ratio tests were not significant ($P > .10$) indicating that variance component estimates were similar for steers classified as high versus low Brahman influence. Likelihood ratio test statistics ranged in value from 0.589 to 4.522 for HCW, FAT, FYG, TLY and MAR. The LRTS for WAR was 7.169 which had a corresponding P-value of 0.0667, indicating that there was only a tendency

Table 7.1 Sample Summary Statistics for DIF and COM models.

Trait	Group	N	MIN	MAX	AVG	STD
HCW	HB	659	117	424	277	42.37
	LB	871	131	403	268	42.17
FAT	HB	658	0.04	2.6	0.73	0.41
	LB	871	0.05	3.1	0.92	0.49
REA	HB	659	36	105	71.6	10.13
	LB	871	44	130	70.3	12.78
WAR	HB	659	18	41	26.2	3.46
	LB	871	17	44	26.5	3.99
FYG	HB	659	1.0	5.0	2.36	0.71
	LB	871	1.0	6.1	2.69	0.89
TLY	HB	659	62	213	142.8	21.03
	LB	871	69	216	135.8	21.30
MAR	HB	659	1.0	5.8	3.64	0.84
	LB	871	1.5	8.3	4.30	0.95
WBS	HB	161	6.2	23.2	11.9	3.53
	LB	702	4.8	22.8	9.6	2.34

for HB and LB groups to have heterogeneous variance component estimates for WAR. Huffman et al. (1990) noted that among steers with zero, 25, 50 and 75 % Brahman influence, carcass weight adjusted ribeye area tended to be larger and more variable among steers with higher levels of Brahman influence. Data presented in chapter four showed, however, that few direct additive genetic effect contrasts for WAR were significant.

Comparison of DIF and COM models for REA and WBS indicated that level of Brahman influence was a significant source of heterogeneity. Estimates of additive genetic, residual and phenotypic variances by level of Brahman influence classification are given in table 7.3. Upon inspection, it appeared that steers in the HB classification had a lower estimate of additive genetic variance (31.213 vs. 64.961 $(cm^2)^2$) for REA than did steers in the LB classification. Conversely, the estimate of additive genetic variance for WBS among HB steers appeared to be larger than that among LB steers (6.180 vs. 0.3912 kg^2). However, the estimates of residual variances for WBS between LB and HB steers appeared to be similar (4.462 and 3.869 kg^2). The heritability estimates derived from these estimates were 0.581 for the HB steers and 0.092 for the LB steers (table 7.4). Tests of heterogeneity among ratios of variance components were not made. Further, standard errors for variance components and genetic parameters are not readily obtainable from MTDFREML, therefore, these parameters were not estimated. The interpretation of these results is that the joint estimates of additive genetic and

Table 7.2 Likelihood Ratio Tests From DIF Versus COM Model Comparisons for Carcass Traits.

Trait	df	LRTS[a]	P[b]
HCW	3	0.884	0.8293
FAT	3	1.063	0.7860
REA	3	16.672	0.0008
WAR	3	7.169	0.0667
FYG	3	0.957	0.8117
TLY	3	0.589	0.8989
MAR	3	4.522	0.2103
WBS	3	53.792	0.0000

a Likelihood ratio test statistic = difference in -2Λ between DIF and COM models.

b $P = P(\chi^2_3 > \text{LRTS} \mid \text{Ho is true})$.

Table 7.3 Estimates of Additive Genetic, Residual and Phenotypic Variances Within Low (LB) and High (HB) Brahman Groups for Ribeye Area (REA) and Warner-Bratzler Shear (WBS) Force.

	REA		WBS	
Estimate	LB	HB	LB	HB
Additive Genetic	64.961	31.213	0.3192	6.180
Residual	24.387	36.383	3.8693	4.462
Phenotypic	89.348	67.596	4.2601	10.642

Table 7.4 Estimates of Heritabilities (h^2) for Ribeye Area (REA) and Warner-Bratzler Shear (WBS) Force Among Low (LB) and High (HB) Brahman Groups.

	h^2	
Trait	LB	HB
REA	0.727	0.462
WBS	0.092	0.581

residual variances among HB and LB steers were different for REA and WBS. Van Vleck et al. (1992) discussed the importance of considering breed heterogeneity in the estimation of interbreed breeding values. They stated that sires within a breed or crossbred group tended to rank similarly due to large differences among breed effects. Their results illustrated that for traits with large breed differences, selection of the proper breed should be made before selection is applied within that breed.

The LB and HB classifications contributed ($P < .001$) to heterogeneity of variance for REA. The additve genetic variance within the LB group was 64.961 $(cm^2)^2$ while the estimate for the HB group was 31.217 $^2(\hat{c}m)$. Residual variance estimates were larger within the HB group relative to the LB group, but the differences were smaller than between estimates of additive genetic variances. Estimates of phenotypic variance for REA within LB and HB groups were 89.348 and 67.596 $(cm^2)^2$, respectively (table 7.3). The heritabilities therefore appeared to be different among the Brahman influence groups: 0.727 for the LB and 0.462 for the HB (table 7.4).

These results indicate that for estimation of interbreed breeding values, heterogeneity of variances in certain carcass traits should be considered, depending on fraction of Brahman influence. If a version of the animal model were implemented to carry out multibreed genetic evaluations for carcass

traits, the model should take into account differences in variance components due to percentage Brahman influence. Simplifications for a multivariate animal model to account for heterogeneous variances could be applied in these cases.

CHAPTER 8

SUMMARY AND IMPLICATIONS

Genetic analyses were conducted on a wide array of cattle types and for a large number of traits. The estimation of genetic parameters precedes the recommendation of selection and breeding programs designed to increase the efficiency of the beef production enterprise. The segmentation of the beef industry has resulted in emphasis being placed by producers on different traits depending on the segment on the beef cycle into which they fit. The traits which most substantially affect profitability often differ among the segments.

Crossbreeding has become the predominant system of mating in the U.S. beef industry. By providing for the use of additive and non-additive genetic variation among breeds, crossbreeding, along with sound selection strategies, can improve production by 20 to 30 percent, or more.

In the Gulf Coast Region of the United States, where a majority of producers are cow-calf oriented, the major product is the weaned beef calf. Therefore, preweaning performance traits are of importance to the profitability of the cow-calf segment. Following weaning, steers and heifers that are managed to produce beef are eventually placed in a feedlot where high concentrate rations are fed prior to slaughter. During this postweaning feedlot phase, profitability is mostly influenced by rate of gain and efficiency of conversion of feed to gain. The product for sale by the packing segment of the beef cycle is the beef carcass, as a whole or as primal and subprimal parts.

The packing segment places profitability emphasis on carcass yield and quality. The discrepancy among traits affecting profitability for each segment of the beef industry has resulted in lack of consistency in the beef product. Few genetic studies have been conducted to investigate the relationships among economically important traits across segments of the beef cycle.

Recent studies which characterize the yield and quality of beef in the industry have indicated that a lack of consistency in the beef product, especially with regard to palatability, has contributed to a substantial loss in profit potential. For example, tenderness has no direct impact on the value of beef, yet consumers rank lack of consistency in tenderness as a primary problem in the desirability of beef. Genetic parameters for carcass traits have been extensively studied, however, further research is needed to estimate the genetic association between carcass traits and early life traits of economic importance such as preweaning growth performance. Also, there is a lack of research which estimates genetic relationships between carcass traits and traits affecting reproductive performance. Also, among genetic parameter estimates for carcass traits, parameters such as genetic correlations among meat quality traits are highly variable. Finally, sound selection decisions cannot be made without consideration of possible genetic antagonisms between traits of economic interest.

The adaptability of the Brahman and heterosis derived from crossbreeding programs involving the Brahman have resulted in extensive use

of *Bos indicus* genetic resources in the Gulf Coast Region, where the performance of the cow herd is of primary importance. Crossbreeding using Brahman produces calves destined for the feedlot and packing phases of the beef industry which have distinct Brahman or zebu characteristics. These characteristics include the presence of excess skin about the neck and underline, an often visible cervico-thoracic hump, and distinct zebu color patterns such as brindling. These visual indicators associated with Brahman breeding often result in price discrimination being applied to Brahman influenced beef calves by the feeding and packing segments due to less desirable yield and quality grades often found among cattle of heavy Brahman influence. Considerable research has indicated that Brahman influence is associated with decreases in marbling (carcass quality) and palatability (tenderness).

The results of the present study indicated that the direct additive genetic effect of Brahman was smaller for marbling and larger for Warner-Bratzler shear force than the average non-Brahman additive genetic effect. Also, the additive genetic effect of the Charolais was larger for slaughter weight, hot carcass weight and total lean yield. Although differences were found to exist among maternal additive genetic effects, these effects were generally smaller than corresponding direct additive genetic effects.

Crossbreeding allows for the use of non-additive genetic variance among breeds, or heterosis. Direct heterosis tended to affect carcass traits

associated with weight and yield to a larger degree than traits associated with carcass quality. In all cases, English (Angus or Hereford) x Brahman direct heterosis levels tended to be larger in magnitude than the other direct heterosis effects. Likewise, direct heterosis effects involving the Brahman were larger and were different from zero more often than direct heterosis effects not involving the Brahman (i.e., English x English and English x Charolais). The effect of total maternal heterosis was generally small and near zero for postweaning growth and carcass traits. However, total maternal heterosis significantly reduced daily gain on ryegrass and total lean yield.

Estimates of variance components and genetic parameters were similar to previous estimates reported in the literature. Heritabilities for carcass traits were mostly moderate to large ($h^2 > .20$) except in the case of Warner-Bratzler shear force, for which the heritability estimate was 0.156. Among postweaning growth traits, heritability was higher for gain on feed than for gain on ryegrass, indicating greater expression of genetic variability on higher versus lower planes of nutrition.

Genetic and phenotypic correlations revealed the high association between increased gain, increased weights and increased carcass yield. Growth and performance traits in the preweaning and postweaning phases were highly correlated with carcass measures of weight and yield. Measures of muscling (ribeye area and carcass weight adjusted ribeye area) were also highly correlated. Most of the variation in total lean yield could be explained

by hot carcass weight. Genetic and phenotypic correlations with marbling score tended to be low (Rg < .25) indicating few possibilities for improvement in marbling score through correlated response to selection. Warner-Bratzler shear force had negative and favorable genetic correlations with increased performance, muscling and weight, but lower and near zero genetic correlations with traits related to fatness. These results indicate that selection for increased performance at any point in the beef cycle would not be expected to be antagonistic to improved tenderness. Also, selection for meat quality (tenderness and/or marbling score), assuming it was practical, would not be expected to be antagonistic to improvement in growth performance or carcass yield.

An analysis of heterogeneity of variance due to percent Brahman influence indicated that variance component estimates were different between low (< 25 %) and high ($\geq$ 25 %) Brahman steers. The additive genetic variance and heritability estimates for ribeye area within low Brahman steers was larger than the corresponding estimate within high Brahman steers. This result may indicate a reduced potential for selection to improve ribeye area in high Brahman steers. However, the direct additive effect of Brahman to reduce total lean yield relative to the average direct additive non-Brahman effect was shown to be more related to differences in hot carcass weight rather than ribeye area. The hypothesis that increased Brahman influence was associated with less muscling was generally unsupported in these data.

Conversely, the additive genetic variance and heritability estimates for Warner-Bratzler shear force was higher within the high Brahman steers compared to the corresponding estimates within the low Brahman steers. Therefore, although mean differences were found which support previous reports that increased Brahman influence was associated with decreased tenderness, these results indicated that greater potential exists within high Brahman steers for selection for improved tenderness. Further research is needed to clarify the optimum approach to improvement in tenderness in cattle with more that 25 percent *Bos indicus* breed composition. The variability in tenderness among these cattle may be of more importance as it becomes increasingly important to improve consistency in beef palatability.

The results of the studies presented here both support previous reports regarding contrasts of fixed genetic effects and estimates of genetic parameters. Further, more research is indicated to estimate genetic associations among economic traits across the diverse segments of the beef industry. Of particular importance among these is the estimation of genetic parameters between carcass traits and traits associated with reproductive performance. Finally, it is necessary to clarify the relative importance of component (hot carcass weight, ribeye area, fat thickness) versus composite (final yield grade, carcass weight adjusted ribeye area, total carcass yield) traits to be included in selection programs designed to improve the efficiency of the beef enterprise. While the importance of the Brahman and other *Bos*

indicus breeds continues to be significant in the U.S. beef industry, data used to study these problems should include cattle with the full range of *Bos indicus* influence.

LITERATURE CITED

Arnold, J.W., J.K. Bertrand, L.L. Benyshek and C. Ludwig. 1991. Estimates of genetic parameters for live animal ultrasound, actual carcass data, and growth traits in beef cattle. J. Anim. Sci. 69:985.

Arnold, J.W., J.K. Bertrand and L.L. Benyshek. 1992. Animal model for genetic evaluation of multibreed data. J. Anim. Sci. 70:3322.

Baker, J.F., C.R. Long and T.C. Cartwright. 1984. Characterization of cattle of a five breed diallel. V. Breed and heterosis effects on carcass merit. J. Anim. Sci. 59:922.

Benyshek, L.L. 1981. Heritabilities for growth and carcass traits estimated from data on Herefords under commercial conditions. J. Anim. Sci. 53:49.

Bertrand, J.K., R.L. Willham and J.P. Berger. 1983. Beef, dairy and beef x dairy carcass characteristics. J. Anim. Sci. 57:1440.

Beede, D.K. and R.J. Collier. 1986. Potential nutritional strategies for intensively managed cattle during thermal stress. J. Anim. Sci. 62:543.

Boldman, K.G., L. A. Kriese, L.D. Van Vleck, C.P. Van Tassell and S.D. Kachman. 1995. A Manual for Use of MTDFREML. A Set of Programs to Obtain Estimates of Variances and Covariances [Draft]. U.S. Dept. of Agriculture, Agricultural Research Service.

Brody, S. 1956. Climatic physiology of cattle. J. Dairy Sci. 39:715.

Carpenter, J.W., A.Z. Palmer, W.G. Kirk, F.M. Peacock and M. Koger. 1961. Slaughter and carcass characteristics of Brahman and Brahman-Shorthorn crossbred steers. J. Anim. Sci. 18:336.

Cesar, S.M. 1984. Effects of Dietary Fat, Season and Breed type on Feedlot Performance and Carcass Characteristics of Beef Steers. Ph.D. Dissertation. Univ. of Florida, Gainesville.

Comerford, J.W., L.L. Benyshek, J.K. Bertrand and M.H. Johnson. 1988. Evaluation of performance characteristics in a diallel among Simmental, Limousin, Polled Hereford and Brahman beef cattle. II. Carcass traits. J. Anim. Sci. 66:306.

Crews, Jr., D.H. 1992. Feedlot Performance and Carcass Characteristics of Crossbred Steers Sired by Brahman, Composite and Simmental Bulls and Fed as Calves and as Yearlings. M.S. Thesis. Univ. of Florida, Gainesville.

Crews, Jr., D.H. "Denny". 1995. Improving Carcass Merit in Cattle with Brahman Breeding. Proc. 27th Beef Improvement Federation Annual Meetings, p. 286. Sheridan, Wyoming.

Crews, Jr., D.H., E.B. Moser and D.E. Franke. 1995. A multivariate approach for describing carcass merit in beef cattle. J. Anim. Sci. 73 (Suppl. 1):235 (Abstr.)

Crews, Jr., D.H. "Denny". 1996. Targets for Beef Cattle Improvement: Selection for Meat Quality. Proc. 28th Beef Improvement Federation Annual Meetings, p. 207. Birmingham, Alabama.

Crockett, J.R., F.S. Baker, J.W. Carpenter and M. Koger. 1979. Preweaning, feedlot, and carcass characteristics of calves sired by continental, Brahman and Brahman-derivative sires in subtropical Florida. J. Anim. Sci. 49:900.

Crouse, J.D., L.V. Cundiff, R.M. Koch, M. Koohmaraie and S.C. Seideman. 1989. Comparisons of *Bos indicus* and *Bos taurus* inheritance for carcass beef characteristics and meat palatability. J. Anim. Sci. 67:2661.

Cundiff, L.V. and K.E. Gregory. 1968. Improvement of Beef Cattle Through Breeding Methods. USDA-ARS Res. Bull. No. 196. NC-1 Regional Beef Cattle Breeding Project. Lincoln, Nebraska.

Cundiff, L.V. 1970. Experimental results on crossbreeding cattle for beef production. J. Anim. Sci. 30:694.

Cundiff, L.V., R.M. Koch and K.E. Gregory. 1984. Characterization of biological types of cattle. IV. Postweaning growth and feed efficiency. J. Anim. Sci. 58:312.

DeRouen, S.M., D.E. Franke, T.D. Bidner and D.C. Blouin. 1992. Direct and maternal genetic effects for carcass traits in beef cattle. J. Anim. Sci. 70:3677.

Elzo, M.A. and T.R. Famula. 1985. Multibreed sire evaluation procedures within a country. J. Anim. Sci. 60:942.

Finch, V.A. 1986. Body temperature in beef cattle: its control and relevance to production in the tropics. J. Anim. Sci. 62:531.

Franke, D.E. 1980. Breed and maternal heterosis effects of American Zebu cattle. J. Anim. Sci. 50:1206.

Garrick, D.J., E.J. Pollak, R.L. Quaas and L.D. Van Vleck. 1989. Variance heterogeneity in direct and maternal weight traits by sex and percent purebred for Simmental-sired calves. J. Anim. Sci. 67:2515.

Gregory, K.E., L.V. Cundiff and R.M. Koch. 1995. Genetic and phenotypic (co)variances for growth and carcass traits of purebred and composite populations of beef cattle. J. Anim. Sci. 73:1920.

Gould, L.S. and D.H. "Denny" Crews, Jr. 1996. CANAGE: A Set of Programs to Obtain Coefficients for Additive and Non-Additive Genetic Effects. Univ. of Nebraska, Lincoln, Nebraska.

Habet, O. 1996. Rotational Crossbreeding of Beef Cattle: System Differences and Genetic Effects. M.S. Thesis. Louisiana State Univ., Baton Rouge.

Harville, D.A. 1977. Maximum likelihood approaches to variance component estimation and to related problems. J. Amer. Stat. Assoc. 74:200.

Henderson, C.R. 1963. Selection index and expected genetic advance. In: Statistical Genetics in Plant Breeding. NAS-NRC publ. 982.

Henderson, C.R. 1984. Application of Linear Models in Animal Breeding. U. Guelph, Guelph, Ontario, Canada.

Huffman, R.D., S.E. Williams, D.D. Hargrove, D.D. Johnson and T.T. Marshall. 1990. Effects of percentage Brahman and Angus breeding, age-season of feeding and slaughter end point on feedlot performance and carcass characteristics. J. Anim. Sci. 68:2243.

Johnson, D.D., R.D. Huffman, S.E. Williams and D.D. Hargrove. 1990. Effects of percentage Brahman and Angus breeding, age-season of feeding and slaughter end point on meat palatability and muscle characteristics. J. Anim. Sci. 68:1980.

Koch, R.M. 1978. Selection in beef cattle III. Correlated response of carcass traits to selection for weaning weight, yearling weight and muscle score in cattle. J. Anim. Sci. 47:142.

Koch, R.M., M.E. Dikeman, and J. D. Crouse. 1982. Characterization of biological types of cattle (cycle III): III. Carcass composition, quality and palatability. J. Anim. Sci. 54:35.

Koch, R.M., L.V. Cundiff and K.E. Gregory. 1982. Heritabilities and genetic, environmental and phenotypic correlations of carcass traits in a population of diverse biological types and their implications in selection programs. J. Anim. Sci. 55:1319.

Koch, R.M., M.E. Dikeman, H. Grodzki, J.D. Crouse and L.V. Cundiff. 1983. Individual and maternal genetic effects for beef cattle carcass traits of breeds representing diverse biological types (cycle I). J. Anim. Sci. 57:1124.

Lamb., M.A., O.W. Robison and M.W. Tess. 1990. Genetic parameters for carcass traits in Hereford bulls. J. Anim. Sci. 68:64.

Long, C.R. and K.E. Gregory. 1975. Heterosis and management effects on carcass characteristics of Angus, Hereford and reciprocal cross cattle. J. Anim. Sci. 41:1572.

Long, C.R. 1980. Crossbreeding for beef production: Experimental results. J. Anim. Sci. 51:1197.

Lopes, L.H. 1986. Effects of Diet and Season on Feedlot Performance of Hereford and Brahman-Hereford Crossbred Steers. M.S. Thesis. Univ. of Florida, Gainesville.

MacNeil, M.D., L.V. Cundiff, C.A. Dinkel and R.M. Koch. 1984. Genetic correlations among sex-limited traits in beef cattle. J. Anim. Sci. 58:1171.

MacNeil, M.D., D.R.C. Bailey, J.J. Urick, R.P. Gilbert and W.L. Reynolds. 1991. Heritabilities and genetic correlations for postweaning growth and feed intake of bulls and steers. J. Anim. Sci. 69:3183.

Marshall, D.M. 1994. Breed differences and genetic parameters for body composition traits in beef cattle. J. Anim. Sci. 72:2745.

McDowell, R.F. 1958. Physiological approaches to animal climatology. J. Heredity 49:52.

Meyer, K. 1985. Maximum Likelihood estimation of variance components for a multivariate mixed model with equal design matrices. Biometrics 41:153.

Mies, W.L. 1996. The Gulf Coast Miracle. Proc. 28th Beef Improvement Federation Annual Meetings. Birmingham, Alabama.

Morgan, J.B., J.W. Savell, D.S. Hale, R.K. Miller, D.B. Griffin, H.R. Cross and S.D. Shackelford. 1991. National beef tenderness study. J. Anim. Sci. 69:3274.

National Cattlemens Association (NCA). 1992. Executive Summary National Beef Quality Audit. National Cattlemens Association, Englewood, Colorado.

Nunez-Dominguez, R., L.D. Van Vleck and K.G. Boldman and L.V. Cundiff. 1993. Correlations for genetic expression for growth of calves of Hereford and Angus dams using a multivariate animal model. J. Anim. Sci. 71:2330.

Olson, T.A., 1987. Feedlot performance and carcass characteristics of Senepol-sired steers from Zebu x *Bos taurus* crossbred dams. Proc. Intl. Senepol Res. Sym., Agri. Exp. Sta., Univ. of the Virgin Isl., St. Croix 1:109.

Peacock, F.M., M. Koger, A.Z. Palmer and J.W. Carpenter. 1982. Feedlot performance and carcass traits of Angus, Brahman, Charolais and reciprocal F_1 crosses of the three breeds. Tech. Bull. No. 814. Univ. of Florida, Gainesville.

Reynolds, W.L., J.J. Urick, D.A. Veseth, D.D. Kress, T.C. Nelson and R.E. Short. 1991. Genetic parameters by son-sire covariances for growth and carcass traits of Hereford bulls in a nonselected herd. J. Anim. Sci. 69:1000.

Rodriguez-Almeida, F.A., L.D. Van Vleck, L.V. Cundiff and S.D. Kachman. 1995. Heterogeneity of variance by sire breed, sex and dam breed in 200- and 365-day weights of beef cattle from a top cross experiment. J. Anim. Sci. 73:2579.

Salgado, D. 1995. Estimation of Genetic Parameters for Preweaning Growth Traits of Crossbred Cattle. Ph.D. Dissertation. Louisiana State Univ., Baton Rouge, Louisiana.

Sanders, J.O. and J.C. Paschal. 1987. Postweaning growth and carcass characteristics of Senepol-, Angus-, and Zebu-sired crossbred steers. Proc. Int. Senepol Res. Sym., Agri. Exp. Sta., Univ. of the Virgin Isl., St. Croix 1:123.

Searle, S.R. 1979. Notes on variance component estimation: A detailed account of maximum likelihood and kindred methodology. Paper BU-673-M, Biometrics Unit, Cornell Univ., Ithaca, New York.

Shackelford, S.D., M. Koohmaraie, L.V. Cundiff, K.E. Gregory, G.A. Rohrer and J. W. Savell. 1994. Heritabilities and phenotypic and genetic correlations for bovine postrigor calpastatin activity, intramuscular fat content, Warner-Bratzler shear force, retail product yield and growth rate. J. Anim. Sci. 72:857.

Turner, J.W. 1980. Genetic and biological aspects of Zebu adaptability. J. Anim. Sci. 50:1201.

Urick, J.J., B.W. Knapp, R.L. Hiner, O.F. Pahnish, J.S. Brinks and R.L. Blackwell. 1974. Results from crossing beef x beef and beef x Brown Swiss: Carcass quanitity and quality traits. J. Anim. Sci. 39:292.

USDA. 1989. Official United States Standards for Grades of Carcass Beef. Title 7, Ch. 1, Pt. 54, Sec. 54.102 - 54.107. Washington, D.C.

Van Vleck, L.D. 1992. Selection Index and Introduction to Mixed Model Methods. CRC Press, Boca Raton, Florida.

Van Vleck, L.D., A.F. Hakim, L.V. Cundiff, R.M. Koch, J.D. Crouse and K.G. Boldman. 1992. Estimated breeding values for meat characteristics of crossbred cattle with an animal model. J. Anim. Sci. 70:363.

Van Vleck, L.D. 1994. Prediction error variances for inter-breed EPD's. Proc. 4th Genetic Prediction Workshop. Kansas City, Missouri.

Veseth, D.A., W.L. Reynolds, J.J. Urick, T.C. Nelson, R.E. Short and D.D. Kress. 1993. Paternal half-sib heritabilities and genetic, environmental, and phenotypic correlation estimates from randomly selected Hereford cattle. J. Anim. Sci. 71:1730.

Warwick, E.J. 1958. Effects of high temperatures on growth and fattening in beef cattle, sheep and hogs. J. Heredity 49:69.

Wheeler, T.L., J. W. Savell, H.R. Cross, D.K. Lunt and S.B. Smith. 1990. Mechanisms associated with the variation in tenderness of meat from Brahman and Hereford cattle. J. Anim. Sci. 68:4206.

Whipple, G.M., M. Koohmaraie, M.E. Dikeman, J.D. Crouse, M.C. Hunt and R.D. Klemm. 1990. Evaluation of attributes that affect muscle tenderness in *Bos taurus* and *Bos indicus* cattle. J. Anim. Sci. 68:2716.

Wilson, D.E., R.L. Willham, S.L. Northcutt and G.H. Rouse. 1993. Genetic parameters for carcass traits estimated from Angus field records. J. Anim. Sci. 71:2365.

Woodward, B.W., E.J. Pollak and R.L. Quaas. 1992. Parameter estimation for carcass traits including growth information of Simmental beef cattle using restricted maximum likelihood with a multiple-trait model. J. Anim. Sci. 70:1098.

Young, L.D., L.V. Cundiff, J.D. Crouse, G.M. Smith and K.E. Gregory. 1978. Characterization of biological types of cattle. VIII. Postweaning growth and carcass traits of three-way cross steers. J. Anim. Sci. 46:1178.

Zinn, D.W., R.M. Durham and H.B. Hendrick. 1970. Feedlot and carcass characteristics of steers and heifers as influenced by days on feed. J. Anim. Sci. 31:302.

VITA

D.H. "Denny" Crews, Jr., was born November 16, 1967, in Avon Park, Florida, to Mr. and Mrs. D. Horace Crews. He was raised on the family agricultural enterprise, involving commercial cattle production, citrus and farming. After being graduated Valedictorian of the Frostproof High School class of 1985, he attended South Florida Community College, Avon Park, Florida, and graduated with the A.A. degree in May, 1987. He received the Bachelor of Science degree in May, 1989 from the University of Miami, Coral Gables. After one year of employment, he entered graduate school at the University of Florida, Gainesville in August, 1990. The degree Master of Science in Animal Science (Beef Cattle Breeding and Management) was conferred in August, 1992. He pursued further graduate study in Animal Science at Texas A&M University prior to enrolling at Louisiana State University in June, 1994, to pursue the doctor of philosophy degree in Animal Science with emphasis in Beef Cattle Breeding and Genetics and minors in both Experimental Statistics and Interdisciplinary Studies in Genetics.

DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: D. H. "Denny" Crews, Jr.

Major Field: Animal & Dairy Sciences

Title of Dissertation: Genetic Components of (Co)variance for Postweaning Growth, Carcass Composition and Meat Quality Traits Among Brahman-Influenced Beef Steers

Approved:

D E Franke
Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

David W. Forrest

William G. Hevel

Edgar Barry Moser

Paul L. Hames

Date of Examination:

10-30-96